

THE LIFE CYCLE AND BEHAVIOR
OF CERCOLEIPUS COELONOTUS
(ACARINA: MESOSTIGMATA)

*Including a Survey of Phoretic Mite Associates
of California Scolytidae*

BY
D. N. KINN

UNIVERSITY OF CALIFORNIA PUBLICATIONS IN ENTOMOLOGY
Volume 65

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UNIVERSITY OF CALIFORNIA PUBLICATIONS IN ENTOMOLOGY
ADVISORY EDITORS: J. N. BELKIN, R. M. BOHART, PAUL DEBACH,
R. L. DOUTT, E. I. SCHLINGER, E. A. STEINHAUS

Volume 65

Approved for publication July 30, 1970

February 5, 1971

Price, \$2.50

UNIVERSITY OF CALIFORNIA PRESS
BERKELEY AND LOS ANGELES
CALIFORNIA



UNIVERSITY OF CALIFORNIA PRESS, LTD.
LONDON, ENGLAND

ISBN: 0-520-09379-8

LIBRARY OF CONGRESS CATALOG CARD No.: 78-632911

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PRINTED IN THE UNITED STATES OF AMERICA

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INTRODUCTION

BARK BEETLES kill more standing timber than any other agent, including fire (U.S.D.A. Forest Resource Report No. 14, 1958), and thus constitute a major threat to one of our important natural resources. Since it is often impractical or undesirable to treat infestations chemically (Carson, 1962; Rudd, 1964), more attention is now being given to the study of natural control agents (Beal, 1965). McGugan (1962) urged support of research dealing with natural enemies of forest pests and stressed their importance in the overall population dynamics of pest species. Also, Voûte (1964) has pointed out the necessity of studying noxious insects under endemic as well as epidemic conditions.

Mites are an important group of natural control agents which have been largely overlooked (Rust, 1933). Samšínák (1966) stated that the use of parasitic mites, such as *Pyemotes* spp., to control forest pests appears less dangerous than the use of some chemical substances. Therefore, the accumulation of basic ecological information on forest acarines may have future application in the augmentation of these natural control agents.

Of the numerous mites associated with *Ips confusus* (LeConte) several belong to the Trignyaspida of the suborder Mesostigmata. Because of the scant knowledge of most species and because of the possible importance of mites on the population dynamics of bark beetles, one species, *Cercoleipus coelonotus* Kinn, was selected for this investigation (Kinn, 1970).

FOREST ACARINES

Perhaps the most thoroughly studied of the forest acari have been soil mites. Mites are the most numerous of all soil metazoans (Eaton and Chandler, 1942), being most abundant in the upper 7 to 10 cm of humus and leaf litter (Wallwork, 1958). Soil oribatids feed upon dead collembola and earthworms, fungi, and fallen leaves and twigs (Birch and Clark, 1953), thus reducing these materials into crude mineral and organic matter (Jacot, 1932; Crossley and Witkamp, 1964). The high density and feeding habits of these organisms are therefore of considerable importance to soil fertility (Hartenstein, 1962).

This study is based on a thesis submitted in June, 1969, to the Graduate Division, University of California, Berkeley, in partial fulfillment of the requirements for the degree of Doctor of Philosophy in entomology. The research was supported in part by a predoctoral fellowship grant from the United States Public Health Service, and travel funds were provided by the Walker and Surdna Foundations, the California Division of Forestry and various forest industries.

The importance of these organisms to the forest economy extends far beyond soil fertility. Some mites, such as those of the families Eriophyidae and Tetranychidae, cause direct damage to trees and others may vector pathogens. Jacot (1934, 1936) suggested that tyroglyphid mites found associated with *Scolytus multistriatus* Marsh may carry spores of *Ceratocystis ulmi* (Buis.) Moreau and thus may be a contributing factor in the spread of Dutch elm disease. Deutonymphs of *Histiogaster fungivorax* Jacot, *Monieziella arborea* Jacot, and *Tyroglyphus* sp. carry the spores of *Ceratocystis ips* (Rumbold) on their legs and setae. Microscopic examination of mites removed from bark beetles of the genus *Ips*, and cultures made from them, proved that spores of *C. ips* can be disseminated by mites (Leach, Orr, and Christensen, 1934).

On the other hand, mites, along with insect parasitoids, have been implicated in the termination of an outbreak of *Dendroctonus frontalis* Zimm. in Texas (Beal, 1965). In laboratory rearings up to 62 percent of the first brood emerging from logs carried mites (Hetrick, 1940). Fronk (1947) found six species of mites associated with *D. frontalis*. Of these, *Histiogaster carpio* (Kramer) and a *Parasitus* sp. were observed to feed upon the beetle larvae. Moser (1965, personal communication) has found over sixty mite species associated with trees infested with *D. frontalis* and *Ips* spp.

The value of mites in the control of forest pests has never been fully determined (Samšičák, 1967). Rust (1933) found numerous individuals of four species of mites associated with *Ips pini* (Say). Of these, a species of *Parasitus* [*Iponemus truncatus* (Ewing) according to Lindquist (1969)] was observed to devour from 10 to 85 percent of the eggs of this beetle. Rust (1933) suggested that an average of 50 percent of some bark beetle broods may be destroyed by mites. Up to 33 percent of the larvae of *Dendroctonus pseudotsugae* Hopk. were destroyed by a complex of mites consisting of *Calvolia* sp., *Digamasellus quadrisetus* (Berl.), *Lasioseius* sp., *Parasitus* sp., and *Uropoda* sp. (Walters and Campbell, 1955). Since the parent adults are relatively free of mites after establishing the first brood, predation was found to be considerably less on the second brood.

Not all of the mites associated with bark beetles are predaceous on the beetles. In the past these have been divided into three categories (Wichmann, 1927; Riley, 1952): (1) those using the insect only as a means of dispersal, (2) those which are predatory on other mites associated with the insect, and (3) true parasitic species. The last category should also contain mites predaceous upon the insect. Mites which feed upon predaceous, parasitic, or inquiline organisms present in bark beetle galleries may contribute to a higher survival of the beetle brood. Mycetophagous mites may aid bark beetles of the genus *Ips* and other polygamous genera by preventing fungi from blocking the galleries. Some mites, such as *Pyemotes ventricosus* (Newp.), attack both the beetle larvae and the larvae of hymenopterous parasites (Schvester, 1957), and the trombidid, *Atomus rhopalicus* Vercammen-Grandjean and Popp, destroys the chalcid, *Rhopalicus tutela* Walker, a parasite of *Ips typographus* Linn. (Vercammen-Grandjean and Popp, 1967). Other mites feed on parasitic nematodes. Massey (1962) noted that *Ips confusus* (LeConte) infested with *Contortylenchus elongatus* (Massey) had reduced egg productivity, and Beal (1965) claimed nematodes were largely responsible for

terminating an outbreak of *Scolytus ventralis* LeConte in New Mexico. However, nematodes and mites have not been shown to be effective controlling agents of *Dendroctonus terebrans* (Oliv.) (Smith and Lee, 1957). In some situations nematodes which feed upon fungi disappear when competing with fungus-feeding mites (Baker, Brown, and James, 1954). Gossard (1913) concluded that the many mites found in the galleries and clinging to *Phloeotribus liminaris* (Harris) are not parasitic but feed on excrement.

Dendroctonus frontalis adults have been laden with as many as forty uropodid mites and as a result were unable to fly (Fronk, 1947). Atkins (1959, 1961) found that mites of the genera *Digamasellus*, *Vidia*, and *Uropoda* had no effect on the duration of flight of *D. pseudotsugae*. However, they did have an effect on wing-beat frequency when clustered at the tips of the elytra (Atkins, 1960). It was suggested that the mites acted as a loading mechanism reducing the wing-beat frequency and thus may affect the distance of flight.

Mites have long been known to vector diseases of man, various animals and plants (Green, 1957). However, until recently, they were not known to vector pathogens of insects. Samšiniák (1964) suggested that anoetid and acarid mites, which often feed on the bodies of dead insects, come in contact with spores of insect disease organisms. He showed that *Tyrophagus putrescentiae* (Schrank) transmitted *Beaveria bassiana* (Bals.-Criv.) Vuill. from *Galleria mellonella* Linn. killed by this fungus to healthy insects of the same species. The mites are not harmed by the fungus. A similar role may be played by some of the Acaridei as associated with bark beetles.

MITE-BARK BEETLE ASSOCIATES

As early as 1880, Haller noted that of all the insect orders, the Coleoptera are the most heavily infested with mites. Löw (1867) and Lucus (1867) reported finding a small gamasid mite associated with *Hylesinus fraxini* Fab. Haller (1880) mentioned that a *Uropoda* sp. was found in association with dead scolytid larvae and pupae. Mites of the genera *Seius* and *Bdella* have been reported from the galleries of *D. pseudotsugae* (Chamberlin, 1918), and Swaine (1918) observed that some bark beetles in Canada are heavily parasitized by mites. Mites of the genus *Seius* attack all stages of *Pityogenes hopkinsi* Swaine (Blackman, 1915).

Much of the literature dealing with mites associated with bark beetles consists of taxonomic descriptions and synoptic lists (Vitzthum, 1923, 1926; Kleine, 1944; Cooreman, 1963; Thatcher, 1960). Others only mention that mites are associated with a given species (Kabir and Giese, 1966; Chodjaï, 1963). However, from such observations it is apparent that mites from diverse families are associated with bark beetles. Hunter and Davis (1963) found six mite species associated with eight species of *Ips*. These belong to the mesostigmatid families Digamasellidae and Uropodidae, the trombidiform families Tarsonemidae, Pyemotidae, and Ereynetidae, and the sarcoptiform family Anoetidae. Stark and Borden (1965) collected mites of the families Uropodidae, Ascidae, Tarsonemidae, Pyemotidae, Ereynetidae, and several Oribatei from the galleries of *S. ventralis*. It has been reported that fifteen species of mites are associated with *Dendroctonus ponderosae* Hopk. (Anonymous, 1965).

MESOSTIGMATA

Ascidae (= Blattisocidae = Aceosejidae)

Many species of *Proctolaelaps* are associated with bark beetles. The feeding habits of these mites have been little studied, but their relationship with the insect host must vary considerably since several species may coexist with one beetle species (Linquist and Hunter, 1965). *Proctolaelaps xyloteri* Sams. is found on *Trypodendron lineatum* Oliv. (Novak, 1960; Samšiniák, 1960). Up to one-third of *T. lineatum* overwintering in the soil had mites attached to them, most of which were *P. xyloteri*, and it has been suggested that this mite may be responsible for part of the observed 30 to 50 percent brood mortality (Novak, 1960). *Proctolaelaps eccoptogasteris* (Vitz.) has been observed to destroy completely all the eggs of *Phloeotribus scarabaeoides* (Bern.) deposited in a single gallery (Russo, 1938).

Lasioseius ometes (Oudemans) has been found associated with *Scolytus laevis* Chapuis, *S. mali* Bechst., and *Hylesinus fraxini* (Vitzthum, 1923; Kielezewski and Michalski, 1962). Vitzthum (1926) observed *L. ometes* consume a protonymph of *Dendrolaelaps cornutus* (Kramer). *Lasioseius hystrix* Vitzthum has been found associated with *Dendroctonus micans* (Kugelann), *Hylastes ater* Park, and *Dryocoetes autographus* Ratz. (Willmann, 1956). Hirschmann and Rühm (1954) claim *L. hystrix* and *L. rotundas* Hirsch. live on beetle excrement, fungi, and nematodes in the galleries of *Ips typographus*.

Digamasellidae (= Ascaidae)

The genus *Digamasellus* is widely distributed, but their principal habitat is the galleries of bark beetles attacking both deciduous and coniferous trees (Hirschmann, 1954a). Thalenhorst (1958) reported that *D. quadrisetus* (Berl.) is an egg predator of *Ips typographus*, but Hirschmann and Rühm (1955) indicated that it is omnivorous, acting as a sanitizer in the gallery system by feeding on fungi, excrement, and nematodes. Womersley (1954) described two species associated with *Ips* in Australia but did not indicate the nature of the association. Quaschik (1953) and Kielezewski and Balazy (1966) found digamasellids feeding on the eggs of *I. typographus* and *I. amitinus* Eichh. and Boss (1967) observed digamasellids feeding on *I. pilifrons* Swaine. *Digamasellus quadrisetus* nymphs and adults feed on the eggs and larvae of *I. confusus* (Kinn, 1967a). Parasitoid and veigaiid mites have been reported preying upon digamasellids (Hirschmann, 1954b).

Parasitidae

Hse (1964) found that a *Eugamasus* sp. associated with *Dendroctonus frontalis*, *Ips calligraphus* (Germ.) and *I. avulsus* (Eichh.) will feed upon ~~nematodes and~~ most of the other mite species found in the gallery system. Others (Fronk, 1947; Rust, 1933; Walters and Campbell, 1955) have observed mites of the genus *Parasitus* preying upon bark beetles.

Macrochelidae

Macrocheles boudreauxi Krantz is found in the galleries of *Dendroctonus frontalis*, *D. terebrans*, *Ips avulsus*, *I. calligraphus* and *I. grandicollis* (Eichh.) where it feeds upon digamasellids, cheyletids, and nematodes (Krantz, 1965).

Uropodidae

This family contains some of the most frequently encountered species phoretic on adult bark beetles. Ewing (1920) observed *Uropoda longisetosa* Ewing in the galleries of *Monarthrum scutellare* (LeConte) in *Quercus agrifolia* Née in California. Species in the genera *Uropoda* (Fronk, 1947; Atkins, 1959; Walters and Campbell, 1955; Vitzthum, 1923, 1926; Kaston, 1939), *Pseudouropoda* (Novak, 1960; Hirschmann and Rühm, 1953) and *Leiodinychus* (Hse, 1964) have been reported from bark beetle galleries. It is commonly thought that most of these mites feed upon the fungi growing in the beetle galleries.

Laelapidae and Dermanyssidae

Hadorn (1933) found *Laelaps agilis* Koch, which normally lives on rodents, phoretic on adult *Trypodendron lineatum* hibernating in the soil. He believes this species may suck the hemolymph of the insect. *Hypoaspis krantzi* Hunter is associated with *Dendroctonus frontalis* and *Ips calligraphus* (Hunter, 1967), but the nature of its association is unknown. Boss (1967) observed *Hypoaspis* sp. feeding on *Histiogaster arborsignum* Woodring.

Celaenopsidae

Pleuronectocelaeno austriaca Vitz. occurs in the galleries of *Pityogenes* sp. (Trägårdh, 1941) and *Scolytus laevis* (Vitzthum, 1926). *Celaenopsis cuspidata* (Kramer) is also associated with *S. laevis* (Vitzthum, 1926). *Pleuronectocelaeno drymoecetes* Kinn has been recently described from the galleries of several species of *Ips* and *Dendroctonus frontalis* in North and Central America (Kinn, 1968).

Cercomegistidae and Schizogyniidae

In addition to *Cercoleipus coelonotus*, *Cercomegistus evonicus* Kinn has been taken from the galleries of *Ips confusus* (Kinn, 1967b). *Choriarchus reginus* Kinn is found in the galleries of *Phloeosinus punctatus* LeConte, *P. sequoiae* Hopk. and *Pseudohylesinus grandis* Swaine (Kinn, 1966).

ELEUTHERENGONA AND TARSONEMINI

Cheyletidae

Speiser (1913) noted that many insects not only transport parasitic mites, but also acarine predators of these mites. *Mexcheles virginianensis* (Baker) associated with *Dendroctonus frontalis* (Baker, 1949) and *Chelacheles michalskii* Samšiniák with *Scolytus multistriatus* and *S. pygmaeus* Fab. (Samšiniák, 1962) are examples of such predaceous mites. Unlike these *Nodele coccineae* Thewke and Enns is predaceous on the larvae of *Pseudopityophthorus minutissimus* (Zimm.) (Thewke and Enns, 1968).

Ereynetidae

Ereynetoides scutulis Hunter was described from specimens found in the galleries of *Ips calligraphus* in *Pinus taeda* Linn. (Hunter, 1964). It has also been found on *I. confusus*, *I. plastographus* (LeConte), *I. pini*, *I. amiskweinsis* G. Hopp., *I. latidens* LeConte and *Dendroctonus brevicornis* LeConte, all from the western United States (Kinn, unpublished data).

Tarsonemidae

In his study of *Ips typographus* and *I. amitinus*, Gäbler (1947) found up to 90 percent of the beetle eggs consumed by *Iponemus gaebleri* (Schaarschmidt). Bombosch (1954) working with *I. typographus*, found only 2 percent of 1414 eggs consumed by *I. gaebleri* and Thalenhorst (1958) never observed high egg mortality caused by this mite. Hirschmann and Rühm (1954) also support this view. Kielczewski (1965) and Balazy and Kielczewski (1966) found up to 10 percent of *I. typographus* eggs destroyed by *I. gaebleri*.

Lindquist and Bedard (1961) attributed *Iponemus confusus* (Lindquist and Bedard) with destroying up to 50 percent of the eggs of *Ips confusus*. *Iponemus* spp. are almost always present in host galleries and egg niches (Lindquist, 1964) and at times the phoretic females are also quite abundant. As many as 80 *Iponemus plastographus* (Lindquist and Bedard) females have been taken from a single *Ips plastographus* (LeConte) adult (Lindquist and Bedard, 1961). Boss (1967) listed the *Iponemus* spp. associated with *Ips* spp. in the Rocky Mountain states and Lindquist (1969) reviewed all the Holarctic tarsonemid mites parasitizing eggs of ipine bark beetles. *Pseudotarsonemoides spinitarsus* Hirst is found on *Scolytus destructor* Oliv. (Hirst, 1923), *P. innumerabilis* Vitz. in the galleries of *Pityogenes bistridentatus* Eichh. (Vitzthum, 1923), and *P. eccoptogasteris* Vitz. from *Scolytus pygmaeus* Fab. and *S. multistriatus* (Vitzthum, 1926). *Tarsonemus moseri* Smiley and *Heterotarsonemus lindquisti* Smiley have been collected from the galleries of *Dendroctonus frontalis* (Smiley, 1967, 1969).

Pyemotidae

Pyemotes ventricosus is the most ubiquitous mite species associated with bark beetles. However, many of the cases of parasitism by *P. ventricosus* probably should be attributed to *P. scolyti* Oudemans, since the two are difficult to distinguish (Schvester, 1957). These mites inject a toxin into their prey which inhibits neuromuscular activity but preserves metabolic activity (Weiser and Slama, 1964), thus preserving the food source.

Hensel (1875) noted *Pyemotes ventricosus* killing the larvae of a bark beetle, probably a species of *Scolytus*. *P. ventricosus* has also been reported attacking the larvae of *Dendroctonus pseudotsugae* (Chamberlin, 1939) and all stages of *Scolytus ventralis* (Struble, 1937, 1957; Stevens, 1956). Russo (1931) reported that larvae of *S. amygdali* (Guerr.) are killed by *P. ventricosus* and Britton (1934) found this mite parasitizing *S. destructor*, but he did not believe they exerted a strong controlling force on the beetle population. Russo (1938) observed both *P. ventricosus* and *P. scolyti* attacking *Phloeotribus scarbaeoides*, and

Schvester (1957) found both species in the galleries and on the adults of *Scolytus rugulosus* Ratz. Previously, Voukassovitch (1947) reported finding *Pyemotes ventricosus* attacking *S. rugulosus*. Although whole populations of *S. rugulosus* reared in the laboratory were at times destroyed by *P. ventricosus*, Schvester (1957) thought its value as a natural control agent in the field was extremely limited. *P. ventricosus* also attacks *Chaetoptelius vestitus* (Muls. and Rey) and a *Hypoborus* sp. (Russo, 1926; Picard, 1919). Unlike *P. scolyti*, *P. ventricosus* will also attack the larvae of hymenopterous parasitoids (Schvester, 1957). Struble (1942) observed *P. ventricosus* killing larvae of the ostomatid *Temnochila vire-scens chlorodia* (Fab.). An unidentified species of *Pyemotes* is reported to be a parasite of the larvae and pupae of *S. mali* and *S. rugulosus* (Sámal, 1931), and Beal and Massey (1945) found an unidentified pyemotid associated with *Ips grandicollis* (Eichh.). *Pyemotes dryas* Vitz. feeds on the larvae and eggs of *Hylurgopinus rufipes* (Eichh.) (Kaston, 1939).

Weiser (1963) discussed mass rearing *Pyemotes scolyti* as a possible biological control agent, and Beaver (1967) stated that *P. scolyti* would be a promising biological control agent for *Scolytus scolytus* (Fab.) and *S. multistriatus* providing a means of increasing its dispersal could be found. Kielczewski and Michalski (1962) found *P. scolyti* on numerous species of *Scolytus* and suggested introducing sterile bark beetles carrying phoretic mites into threatened forested areas. *Pyemotes anobii* Krczal has been mentioned as a possible biological control agent for *S. multistriatus* (Stryker and Stone, 1966).

Hunter and Davis (1963) found a *Pygmephorus* species associated with *Ips avulsus*, *I. calligraphus*, and *I. grandicollis*. Reid (1957) found as many as 33 percent of the eggs of *I. pini* and *I. perroti* Sw. with mites he identified as *Pygmephorus* attached to them. However, Lindquist (1969) believes these were actually *I. truncatus*.

In Russia, Redikorzev (1947) described *Paracarophoenax ipidarius* from *I. typographus* and suspected it of being a parasite of this beetle. A species of *Paracarophoenax* has also been found on *I. confusus* in California (Kinn, unpublished data).

Vitzthum (1923, 1926) reported that *Pediculopsis wichmanni* Vitz. feeds upon fungi in the galleries of *Polygraphus polygraphus* Linn. and Francke-Grosmann (1952) suspected that it also fed upon fungi in the galleries of *Ips acuminatus* Gyll. In contrast to these reports, Redikorzev (1947) reported heavy parasitization of *Ips duplicatus* Sahlb. by this mite.

Haliburton (1943) found an unidentified mite, possibly a pyemotid, causing considerable egg mortality to *Ips grandicollis*.

ACARIDEI AND ORIBATEI

Acaridae

Histiogaster arborsignum occurs in the galleries of *Dendroctonus frontalis*, where it may feed on fungal mycelia, frass, and dead arthropods (Woodring, 1963a). *H. carpio* has also been found associated with *D. frontalis* (Fronk, 1947) and *Xyleborus monographus* Fab. (Schedl, 1964); *H. oudemansi* E. and F. Türk

also occurs with *X. monographus* (Schedl, 1964). Jacot (1936) suspected *H. fungivorax*, *Monieziella arborea*, and *Tyroglyphus* sp., all found with *Scolytus multistriatus*, of transporting blue-stain fungi.

Russo (1938) observed *Tyroglyphus siro* (Linn.) and *Rhizoglyphus* sp. attacking various instars of *Phloeotribus scarabaeoides*. *Winterschmidtia crassisetosa* Willmann is also associated with larvae and pupae of *P. scarabaeoides* (Willmann, 1939). A small gray mite identified as a tyroglyphid is reported to be an important enemy of *Ips plastographus* and *I. mexicanus* (Hopk.) (Trimble, 1915, 1924; Struble, 1961). Immature tyroglyphids suck the contents from *Ips* eggs and young larvae. Many eggs, larvae, and pupae of *Dendroctonus frontalis* are reported destroyed by nymphs and adults of a *Thyreophagus* sp. (Anonymous, 1962).

Acarids are preyed upon by Laelapidae, Parasitidae, Ereyneidae, and Macrochelidae which also occur in bark beetle galleries (Woodring, 1963a).

Saproglyphidae

Calvolia kneissli Krausse deutonymphs are found on *Orthotomicus laricis* Fab. (Krausse, 1917), and a *Calvolia* species was found associated with *Dendroctonus pseudotsugae* (Walters and Campbell, 1955). Vitzthum (1920) described *C. circumspectans* from *Ips stebbingi* (Strohmeyer) in Tibet and Wolff (1920) reported finding numerous mites of this genus living parasitically on *Orthotomicus laricis* and *Blastophagus piniperda* (Linn.). Individual beetles were observed carrying more than twenty-five mites.

Adults of *Vidia* sp. have been taken from beneath the elytra of *Dendroctonus pseudotsugae* (Atkins, 1959).

Anoetidae

Deutonymphs of *Histiostoma ovalis* (Muller) are abundant on adult *Ips sexdentatus* Born (Samšínák, 1958) and *Histiostoma gordius* Hunter and Davis is found associated with *Ips avulsus*, *I. calligraphus*, and *I. grandicollis* in Georgia, *I. chagnoni* Sw., *I. perturbatus* (Eichh.) and *I. pini* in Minnesota, and *I. calligraphus* and *I. emarginatus* (LeConte) in Colorado (Hunter and Davis, 1963). *Histiostoma gordius* is believed to be a fungus feeder (Hunter and Davis, 1963). *H. piceae* Scheucher occurs in the galleries of *I. typographus* (Hirschmann and Rühm, 1954).

Woodring (1963b) believes that acarids and anoetids are not primarily predators.

Oribatei

A number of mites belonging to the Oribatei are occasionally found in the galleries of bark beetles (Fronk, 1947; Stark and Borden, 1965). Those usually encountered are Oribatulidae and Haplozetidae, although other families are also represented. On elm, a number of oribatids occur on the bark and in the galleries of *Scolytus multistriatus* where they feed upon fungi, algae, and other organic matter (Jacot, 1934). The Oribatei found with other bark beetles probably play a similar role.

PHORETIC HABITS OF MITES ASSOCIATED WITH BARK BEETLES

Mesostigmata

All the mesostigmatid mites associated with bark beetles are phoretic at one stage in their life cycles. The deutonymph in the Uropodidae, Digamasellidae, and Parasitidae and the adult in the Ascidae, Macrochelidae, Celaenopsidae, Cercomegistidae, and Schizogyniidae are the phoretic forms. With the exception of the Uropodidae, they all attach to the bark beetles by means of the ambulacra, but some also clamp their chelicerae onto setae (Hirschmann and Rühm, 1953). Digamasellids and ascids may be found almost anywhere on the beetle's body. The strong dorsoventral flattening of their bodies enables them to crawl beneath the elytra. Parasitid deutonymphs and trigynaspid adults are usually found on the outer surface of the elytra. The most highly specialized of the mesostigmatid mites for a phoretic existence are the Uropodidae. These mites fasten themselves to the host by means of anal secretions which harden into long, flexible filaments. Sellnick (1939) points out that many species are known only from the stage taken from the insect host. Unfortunately, this is still true, although Michael (1881) stressed the need for observing all stages of a mite species, its life history, and habits in order to avert synonymies.

The behavior of mesostigmatid mites is largely unknown. Cummins (1898) noted that *Uropoda ovalis* Koch, could detect the presence of bacteria from some distance, but no such studies of the Uropodidae found in bark beetle galleries have been undertaken. Olfaction has been found to be an important stimulus affecting phoresy of *Cosmolaelaps* on passalid beetles (Mollin and Hunter, 1964), *Macrocheles muscaedomesticae* (Scopoli) on house flies (Farish and Axtell, 1966), and *Parasitus coleoptratorum* Linn. on geotrupid beetles (Rapp, 1959). Moist environments inhibit and dry environments promote phoresy of *P. coleoptratorum* (Rapp, 1959).

Eleutherengona and Tarsonemini

Adult female cheyletids and erynetids may be found clinging by means of the ambulacra to almost any part of the bark beetles. However, the dorsal surface and declivity seem to be preferred sites. Hunter and Davis (1963) found *Ereynetoides* sp. rarely phoretic on *Ips calligraphus*, but in California they are occasionally abundant on *I. confusus* (Kinn, unpublished data).

Pyemotid adults cling by means of the large claws on legs I to the setae located near the coxal region or at the junction of the pro- and mesothorax (Redikorzev, 1947). Female tarsonemid mites are found predominately on the elytral declivity of emerging *Ips*, and occasionally on the pronotum, elytra, venter of the abdomen, and between the coxae (Lindquist and Bedard, 1961). They are often found also under the elytra of *Dendroctonus* spp. (Kinn, unpublished data). Lindquist and Bedard (1961) noted that *Iponemus* spp. were most abundant on *Ips* early in the emergence cycle.

Acaridei and Oribatei

The Acaridei are the most highly specialized for phoresy of all mites associated

Most acarologists believe that nutrition is the major factor initiating and terminating the hypopal stage of the Acaridae (Woodring, 1963b). However, the anitid hypopal stage can be initiated and terminated by altering the humidity level of the environment (Wallace, 1960). Hypopi are formed when the media begins to desiccate, and when a moist media is again available most hypopi molt to the tritonymph (Woodring, 1963b). Hunter and Davis (1963) suggest that an oothec hypopi leave the beetle in response to a chemical attractant associated with fungi and yeast growth.

Occasionally oribatids are found on various insects but they lack special adaptations for phoresy (Trägårdh, 1943). They are transported by birds in nesting material or are washed off trees by rain and reascend under more favorable conditions (Jacot, 1934).

CONCLUSION

As early as 1880, Haller referred to the great difficulty encountered in attempting to find widely scattered references to insect-mite relationships in the literature. Kleine (1944) reiterated this problem, which has become compounded with time and an increasing interest in these arthropods. In 1925, Escherich stated that our knowledge of this subject is far from being exhausted and this situation remains unchanged today.

A SURVEY OF MITES ASSOCIATED WITH CALIFORNIA SCOLYTIDAE

More species of Scolytidae occur in California than in any other state. They are found in a wide variety of host trees and shrubs and under diverse climatic conditions, ranging from the low coastal fog belt through dry desertlike foothill areas to the alpine habitats of the high Sierra Nevada. Because a knowledge of the minute fauna is almost nonexistent, a survey was undertaken which included as many different species of bark beetles occupying as many geographical areas and host trees as possible.

MATERIALS AND METHODS

Mites associated with various species of bark beetles found in California were collected from: (1) bark beetle specimens in the California Insect Survey collection of the University of California, Berkeley, (2) living beetles collected in the field, (3) beetles emerging from caged log bolts and bark samples, and (4) frass samples scraped from galleries. Most specimens were cleared in Nesbitt's solution and mounted in Hoyer's medium. Others were collected in alcohol and examined under a dissecting microscope.

RESULTS

Mites were collected from thirty-seven species of bark beetles found in California. Only those mites which were known to have a phoretic stage in their life cycle are included, and those which were rarely encountered in scolytid galleries, i.e., Laelapidae, Uropodellidae, Caeculidae, Raphignathidae, and a *Typhlodromus*.

sp. are omitted. Species of Oribatei belonging to the families Haplozetidae, Camisiidae, and Oribatulidae, which are occasionally found in scolytid galleries, are also omitted because they are not phoretic on adult beetles. The incidence of these mites on trees not under attack by scolytids is probably as great as on those killed by bark beetles.

The three lists which follow summarize the records obtained. Doubtful records are preceded by a question mark.

PHORETIC STAGES AND TROPHIC HABITS OF MITE ASSOCIATES

FAMILY AND SPECIES	PHORETIC STAGE	TROPHIC HABIT
Parasitidae		
<i>Eugamasus</i> sp.	Deutonymph	Predaceous
Digamasellidae		
<i>Digamasellus</i> nr. <i>disetus</i>	Deutonymph	Predaceous
<i>Digamasellus quadrisetus</i>	Deutonymph	Predaceous
<i>Digamasellus neocornutus</i>	Deutonymph	Predaceous
Ascidae		
<i>Proctolaelaps</i> spp.	Adult ♀	Predaceous
<i>Lasioseius</i> sp.	Adult ♀	Predaceous
Uropodidae		
Undetermined spp.	Deutonymph	Mycetophagous
Cercomegistidae		
<i>Cercoleipus coelonotus</i>	Adults	Predaceous
<i>Cercomegistus evonicus</i>	?Adults	?Predaceous
Celaenopsidae		
Undescribed genus	?Adults	?Predaceous
<i>Pleuronectocelaeno drymoeetes</i>	Adults	?Predaceous
Schizogyniidae		
<i>Choriarchus reginus</i>	Adults	?Predaceous
Tarsonemidae		
<i>Tarsonemus</i> sp.	Adult ♀	Mycetophagous
<i>Iponemus</i> spp.	Adult ♀	Parasitic
Pyemotidae		
<i>Pyemotes</i> nr. <i>scolyti</i>	Adult ♀	Parasitic
<i>Pygmephorus</i> sp.	Adult ♀	Mycetophagous
<i>Paracarophoenax</i> nr. <i>ipidarius</i>	Adult ♀	Parasitic
Cheyletidae		
<i>Cheletophyes</i> sp.	Adult ♀	Predaceous
Ereynetidae		
<i>Ereynetoides</i> nr. <i>scutulis</i>	Adults	Predaceous
Acaridae		
<i>Tyroglyphus</i> sp.	Deutonymph	Mycetophagous
<i>Histiogaster</i> nr. <i>arborsignum</i>	Deutonymph	Mycetophagous
Saproglyphidae		
<i>Calvolia</i> sp.	Deutonymph	Mycetophagous
Anoetidae		
<i>Histiostoma</i> sp.	Deutonymph	Mycetophagous
Undetermined sp.	Deutonymph	Mycetophagous

MITE-BARK BEETLE ASSOCIATES

PARASITIDAE

Eugamasus sp.

Dendroctonus brevicomis LeConte—*Pinus ponderosa* Laws. and *Pinus coulteri* D. Don.

Dendroctonus ponderosae Hopkins—*Pinus lambertiana* Dougl.

Dendroctonus valens LeConte—*Pinus jeffreyi* Grev. & Balf.

Ips concinnus (Mannerheim)—*Picea sitchensis* (Bong.) Carr.

Ips confusus (LeConte)—*Pinus ponderosa* Laws. and *Pinus monophylla* Torr. & Frém.

Ips emarginatus (LeConte)—*Pinus jeffreyi* Grev. & Balf.

Ips latidens LeConte—*Pinus jeffreyi* Grev. & Balf. and *Pinus lambertiana* Dougl.

DIGAMASELLIDAE

Digamasellus nr. *disetus*

Dendroctonus brevicomis LeConte—*Pinus ponderosa* Laws.

Dendroctonus valens LeConte—*Pinus jeffreyi* Grev. & Balf.

Ips latidens LeConte—*Pinus jeffreyi* Grev. & Balf.

Digamasellus neocornutus Hurlbutt

Dendroctonus brevicomis LeConte—*Pinus ponderosa* Laws.

Digamasellus quadrisetus (Berlese)

Dendroctonus brevicomis LeConte—*Pinus ponderosa* Laws.

Ips calligraphus (Germar)—*Pinus ponderosa* Laws.

Ips confusus (LeConte)—*Pinus ponderosa* Laws., *Pinus monophylla* Torr. &

Frém., *Pinus lambertiana* Dougl. and *Pinus attenuata* Lemm.

Ips latidens (LeConte)—*Pinus jeffreyi* Grev. & Balf. and *Pinus lambertiana* Dougl.

Ips pini (Say)—*Pinus jeffreyi* Grev. & Balf.

Ips plastographus (LeConte)—*Pinus contorta* Dougl.

Ips sabinianae Hopping—*Pinus sabiniana* Dougl.

Phloeosinus punctatus LeConte—*Libocedrus decurrens* Torr.

Phloeosinus sequoiae Hopkins—*Sequoia sempervirens* (D. Don) Endl.

ASCIDAE

Proctolaelaps spp.

Alniphagus aspericollis (LeConte)—*Alnus* sp.

Conophthorus lambertianae Hopkins—*Pinus lambertiana* Dougl.

Dendroctonus brevicomis LeConte—*Pinus ponderosa* Laws.

Dendroctonus jeffreyi Hopkins—*Pinus jeffreyi* Grev. & Balf.

Dendroctonus ponderosae Hopkins—*Pinus ponderosa* Laws.

Dendroctonus valens LeConte—*Pinus jeffreyi* Grev. & Balf.

Ips confusus (LeConte)—*Pinus ponderosa* Laws. and *Pinus monophylla* Torr. & Frém.

Ips latidens LeConte—*Pinus jeffreyi* Grev. & Balf.

- Ips mexicanus* (Hopkins)—*Pinus radiata* D. Don.
Phloeosinus sequoiae Hopkins—*Sequoia sempervirens* (D. Don) Endl.
Pityophthorus carmeliae Swaine—*Pinus torreyana* Parry.
Pseudohylesinus grandis Swaine—*Pseudotsuga menziesii* (Mirb.) Franco.
Scolytus ventralis LeConte—*Abies concolor* (Gord. & Glend.) Lindl.

Lasioseius sp.

- Ips mexicanus* (Hopkins)—*Pinus muricata* D. Don.
Ips plastographus (LeConte)—*Pinus muricata* D. Don.

UROPODIDAE

Undetermined spp.

- Dendroctonus brevicomis* LeConte—*Pinus ponderosa* Laws. and *Pinus coulteri* D. Don.
Hylastes longicollis Swaine—
Hylastes nitidus Swaine—
Hylurgops porosus (LeConte)—
Ips calligraphus (Germar)—*Pinus ponderosa* Laws.
Ips concinnus (Mannerheim)—*Picea sitchensis* (Bong.) Carr.
Ips confusus (LeConte)—*Pinus ponderosa* Laws., *Pinus monophylla* Torr. & Frém. and *Pinus lambertiana* Dougl.
Ips emarginatus (LeConte)—*Pinus jeffreyi* Grev. & Balf.
Ips latidens LeConte—*Pinus lambertiana* Dougl.
Ips mexicanus (Hopkins)—*Pinus radiata* D. Don and *Pinus muricata* D. Don.
Ips plastographus (LeConte)—
Ips sabinianae Hopping—*Pinus sabiniana* Dougl.
Phloeosinus cristatus (LeConte)—*Cupressus sárgenti* Jepson.
Phloeosinus punctatus LeConte—*Libocedrus decurrens* Torr.
Phloeosinus variolatus Br.—*Cupressus sárgenti* Jepson.
Phloeosinus sp.—*Cupressus macrocarpa* Hartw.
Pityokteines sp.—*Abies concolor* (Gord. & Glend.) Lindl.
Pityophthorus sp.—*Pinus jeffreyi* Grev. & Balf.
Pseudohylesinus dispar Blackman—*Abies concolor* (Gord. & Glend.) Lindl.
Scolytus dentatus Bright—*Abies bracteata* D. Don.
Scolytus robustus Blackman—*Abies bracteata* D. Don.
Scolytus ventralis LeConte—*Abies concolor* (Gord. & Glend.) Lindl.

CERCOMEGISTIDAE

Cercoleipus coelonotus Kinn

- ?*Dendroctonus brevicomis* LeConte—*Pinus ponderosa* Laws.
Ips confusus (LeConte)—*Pinus ponderosa* Laws., *Pinus monophylla* Torr. & Frém., *Pinus jeffreyi* Grev. & Balf. and *Pinus lambertiana* Dougl.
Ips montanus (Eichhoff)—*Pinus monticola* Dougl.
? *Ips emarginatus* (LeConte)—*Pinus jeffreyi* Grev. & Balf.

Cercomegistus evonicus Kinn

- Ips confusus* (LeConte)—*Pinus monophylla* Torr. & Frém.

CELAENOPSIDAE

Undescribed genus

Ips confusus (LeConte)—*Pinus monophylla* Torr. & Frém.

Pleuronectocelaeno drymoecetes Kinn

Ips confusus (LeConte)—*Pinus ponderosa* Laws. and *Pinus monophylla* Torr. & Frém.

Ips sabinianae Hopping—*Pinus sabiniana* Dougl.

SCHIZOGYNIIDAE

Choriarchus reginus Kinn

Phloeosinus punctatus LeConte—*Libocedrus decurrens* Torr.

Phloeosinus sequoiae Hopkins—*Sequoia sempervirens* (D. Don) Endl.

Pseudohylesinus grandis Swaine—*Pseudotsuga menziesii* (Mirb.) Franco.

TARSONEMIDAE

Tarsonemus sp.

Dendroctonus brevicomis LeConte—*Pinus ponderosa* Laws.

Ips concinnus (Mannerheim)—*Picea sitchensis* (Bong.) Carr.

Ips confusus (LeConte)—*Pinus ponderosa* Laws. and *Pinus lambertiana* Dougl.

Ips latidens LeConte—*Pinus lambertiana* Dougl.

Ips mexicanus (Hopkins)—*Pinus radiata* D. Don.

Ips pini (Say)—*Pinus jeffreyi* Grev. & Balf.

Ips sabinianae Hopping—*Pinus sabiniana* Dougl.

Pseudohylesinus grandis Swaine—*Pseudotsuga menziesii* (Mirb.) Franco.

Scolytus dentatus Bright—*Abies bracteata* D. Don.

Scolytus praeceps LeConte—

Scolytus robustus Blackman—*Abies bracteata* D. Don.

Scolytus unispinosus LeConte—*Pseudotsuga menziesii* (Mirb.) Franco.

Scolytus ventralis LeConte—*Abies concolor* (Gord. & Glend.) Lindl.

Iponemus spp.

Dendroctonus brevicomis LeConte—*Pinus ponderosa* Laws.

Dendroctonus ponderosae Hopkins—*Pinus ponderosa* Laws.

Ips confusus (LeConte)—*Pinus ponderosa* Laws., *Pinus radiata* D. Don and

Pinus lambertiana Dougl.

Ips pini (Say)—*Pinus jeffreyi* Grev. & Balf.

Ips plastographus (LeConte)—*Pinus contorta* Dougl.

PYEMOTIDAE

Pyemotes nr. *scolyti*

Conophthorus lambertianae Hopkins—*Pinus lambertiana* Dougl.

Ips confusus (LeConte)—*Pinus radiata* D. Don.

Ips mexicanus (Hopkins)—*Pinus radiata* D. Don.

Ips sabinianae Hopping—*Pinus sabiniana* Dougl.

Phloeosinus cristatus (LeConte)—*Cupressus sárgenti* Jepson.

Phloeosinus punctatus LeConte—*Libocedrus decurrens* Torr.

Phloeosinus sequoiae Hopkins—*Sequoia sempervirens* (D. Don).

Phloeosinus rubicundulus Swaine—*Sequoia gigantea* (Lindl.) Decne.

Pithyophthorus sp.—

Pseudohylesinus grandis Swaine—*Pseudotsuga menziesii* (Mirb.) Franco.

Pseudohylesinus nebulosus (LeConte)—*Pseudotsuga menziesii* (Mirb.) Franco.

Scolytus dentatus Bright—*Abies bracteata* D. Don.

Scolytus praeceps LeConte—

Scolytus robustus Blackman—*Abies bracteata* D. Don.

Scolytus ventralis LeConte—*Abies concolor* (Gord. & Glend.) Lindl.

Taenoglyptes pubescens (Hopkins)—

Pygmephorus sp.

Dendroctonus brevicomis LeConte—*Pinus ponderosa* Laws.

Ips calligraphus (Germar)—*Pinus ponderosa* Laws.

Paracarophoenax nr. *ipidarius*

Dendroctonus brevicomis LeConte—*Pinus ponderosa* Laws.

Ips confusus (LeConte)—*Pinus ponderosa* Laws.

Ips plastographus (LeConte)—*Pinus contorta* Dougl.

CHEYLETIDAE

Cheletophyes sp.

Dendroctonus brevicomis LeConte—*Pinus ponderosa* Laws.

Dendroctonus ponderosae Hopkins—*Pinus ponderosa* Laws.

Ips confusus (LeConte)—*Pinus ponderosa* Laws.

Ips latidens LeConte—*Pinus lambertiana* Dougl.

Scolytus dentatus Bright—*Abies bracteata* D. Don.

EREYNETIDAE

Ereynetoides nr. *scutulis*

Alniphagus aspericollis (LeConte)—*Alnus* sp.

Dendroctonus brevicomis LeConte—*Pinus ponderosa* Laws.

Dendroctonus ponderosae Hopkins—*Pinus ponderosa* Laws.

Ips confusus (LeConte)—*Pinus ponderosa* Laws., *Pinus monophylla* Torr. & Frém. and *Pinus attenuata* Lemm.

Ips latidens LeConte—*Pinus jeffreyi* Grev. & Balf.

Ips pini (Say)—*Pinus jeffreyi* Grev. & Balf.

Ips plastographus (LeConte)—

Scolytus dentatus Bright—*Abies bracteata* D. Don.

Scolytus robustus Blackman—*Abies bracteata* D. Don.

Scolytus ventralis LeConte—*Abies concolor* (Gord. & Glend.) Lindl.

ACARIDAE

Histiogaster nr. *arborsignum*

Dendroctonus brevicomis LeConte—*Pinus ponderosa* Laws.

Dendroctonus ponderosae Hopkins—*Pinus ponderosa* Laws.

Ips calligraphus (Germar)—*Pinus ponderosa* Laws.

Ips confusus (LeConte)—*Pinus ponderosa* Laws.

Ips latidens LeConte—*Pinus jeffreyi* Grev. & Balf.

Ips pini (Say)—*Pinus ponderosa* Laws.

Ips sabinianae Hopping—*Pinus sabiniana* Dougl.

Tyroglyphus sp.

Ips confusus (LeConte)—*Pinus ponderosa* Laws.

Phloeosinus sequoiae Hopkins—*Sequoia sempervirens* (D. Don).

Pityophthorus sp.—*Pinus jeffreyi* Grev. & Balf.

SAPROGLYPHIDAE

Calvolia sp.

Dendroctonus brevicomis LeConte—*Pinus ponderosa* Laws.

Ips concinnus (Mannerheim)—*Picea sitchensis* (Bong.) Carr.

Ips latidens LeConte—*Pinus ponderosa* Laws. and *Pinus lambertiana* Dougl.

Ips sabinianae Hopping—*Pinus sabiniana* Dougl. and *Pinus attenuata* Lemm.

Pityophthorus sp.—

Pityophthorus carmeli Swaine—*Pinus torreyana* Parry.

Pityophthorus setosus Blackman—

Pseudohylesinus nebulosus (LeConte)—*Pseudotsuga menziesii* (Mirb.) Franco.

Scolytus dentatus Bright—*Abies bracteata* D. Don.

Scolytus robustus Blackman—*Abies bracteata* D. Don.

Scolytus unispinosus LeConte—*Pseudotsuga manziesii* (Mirb.) Franco.

ANOETIDAE

Histiostoma sp.

Ips calligraphus (Germar)—*Pinus ponderosa* Laws.

Ips confusus (LeConte)—*Pinus ponderosa* Laws.

Ips latidens LeConte—

Ips mexicanus (Hopkins)—*Pinus radiata* D. Don.

Ips pini (Say)—*Pinus contorta* Dougl.

Ips plastographus (LeConte)—*Pinus contorta* Dougl.

Ips sabinianae Hopping—*Pinus sabiniana* Dougl.

Pityophthorus carmeli Swaine—*Pinus torreyana* Parry.

Pseudohylesinus nebulosus (LeConte)—*Pseudotsuga menziesii* (Mirb.) Franco.

Scolytus dentatus Bright—*Abies bracteata* D. Don.

Scolytus robustus Blackman—*Abies bracteata* D. Don.

Scolytus ventralis LeConte—*Abies concolor* (Gord. & Glend.) Lindl.

Undetermined sp.

Dendroctonus brevicomis LeConte—*Pinus ponderosa* Laws.

BARK BEETLE-MITE ASSOCIATES

Alniphagus aspericollis (LeConte)

Proctolaelaps sp.

Ereynetoides nr. *scutulis*

Conophthorus lambertianae Hopkins

Proctolaelaps sp.

Pyemotes nr. *scolyti*

Dendroctonus brevicomis LeConte

Eugamasus sp.

Digamasellus nr. *disetus*

Digamasellus neocornutus Hurlbutt

Digamasellus quadrisetus Berlese

Proctolaelaps sp.

- Uropodidae*—undetermined spp.
Cercoleipus coelonotus Kinn
Tarsonemus sp.
Iponemus sp.
Pygmephorus sp.
Paracarophoenax nr. *ipidarius*
Cheletophyes sp.
Ereynetoides nr. *scutulis*
Histiogaster nr. *arborsignum*
Calvolia sp.
Anoetidae—undetermined spp.
- Dendroctonus jeffreyi* Hopkins
Proctolaelaps sp.
- Dendroctonus ponderosae* Hopkins
Eugamasus sp.
Proctolaelaps sp.
Iponemus sp.
Cheletophyes sp.
Ereynetoides nr. *scutulis*
Histiogaster nr. *arborsignum*
- Dendroctonus valens* LeConte
Eugamasus sp.
Digamasellus nr. *disetus*
Proctolaelaps sp.
- Hylastes longicollis* Swaine
Uropodidae—undetermined spp.
- Hylastes nitidus* Swaine
Uropodidae—undetermined spp.
- Hylurgops porosus* (LeConte)
Uropodidae—undetermined spp.
- Ips calligraphus* (Germar)
Digamasellus quadrisetus Berlese
Uropodidae—undetermined spp.
Pygmephorus sp.
Histiogaster nr. *arborsignum*
Histiostoma sp.
- Ips concinnus* (Mannerheim)
Eugamasus sp.
Uropodidae—undetermined spp.
Tarsonemus sp.
Calvolia sp.
- Ips confusus* (LeConte)
Eugamasus sp.
Digamasellus quadrisetus Berlese
Proctolaelaps sp.
Uropodidae—undetermined spp.
Cercomegistus evonicus Kinn
Cercoleipus coelonotus Kinn
Celaenopsidae—undescribed genus
Pleuronectocelaeno drymoecetes Kinn
Tarsonemus sp.
Iponemus sp.
Pyemotes nr. *scolyti*
Paracarophoenax nr. *ipidarius*
Cheletophyes sp.
Ereynetoides nr. *scutulis*
Histiogaster nr. *arborsignum*
Tyroglyphus sp.
Histiostoma sp.
- Ips emarginatus* (LeConte)
Eugamasus sp.
Uropodidae—undetermined spp.
 ? *Cercoleipus coelonotus* Kinn
- Ips latidens* LeConte
Eugamasus sp.
Digamasellus nr. *disetus*
Digamasellus quadrisetus Berlese
Proctolaelaps sp.
Uropodidae—undetermined spp.
Tarsonemus sp.
Cheletophyes sp.
Ereynetoides nr. *scutulis*
Histiogaster nr. *arborsignum*
Calvolia sp.
Histiostoma sp.
- Ips mexicanus* Hopkins
Proctolaelaps sp.
Lasioseius sp.
Uropodidae—undetermined spp.
Tarsonemus sp.
Pyemotes nr. *scolyti*
Histiostoma sp.
- Ips montanus* (Eichhoff)
Cercoleipus coelonotus Kinn
- Ips pini* (Say)
Digamasellus quadrisetus Berlese

- Tarsonemus* sp.
Iponemus sp.
Ereynetoides nr. *scutulis*
Histiogaster nr. *arborsignum*
Histiostoma sp.
- Ips plastographus* (LeConte)
Eugamasus sp.
Digamasellus quadrisetus Berlese
Lasioseius sp.
 Uropodidae—undetermined sp.
Iponemus sp.
Paracarophoenax nr. *ipidarius*
Ereynetoides nr. *scutulis*
Histiostoma sp.
- Ips sabinianae* Hopping
Digamasellus quadrisetus Berlese
 Uropodidae—undetermined sp.
Pleuronectocelaeno drymoecetes Kinn
Tarsonemus sp.
Pyemotes nr. *scolyti*
Histiogaster nr. *arborsignum*
Calvolia sp.
Histiostoma sp.
- Phloeosinus cristatus* (LeConte)
 Uropodidae—undetermined sp.
Pyemotes nr. *scolyti*
- Phloeosinus punctatus* LeConte
Digamasellus quadrisetus Berlese
 Uropodidae—undetermined sp.
Choriarchus reginus Kinn
Pyemotes nr. *scolyti*
- Phloeosinus sequoiae* Hopkins
Digamasellus quadrisetus Berlese
Proctolaelaps sp.
Choriarchus reginus Kinn
Pyemotes nr. *scolyti*
Tyroglyphus sp.
- Phloeosinus rubicundulus* Swaine
Pyemotes nr. *scolyti*
- Phloeosinus variolatus* Br.
 Uropodidae—undetermined sp.
- Phloeosinus* sp.
Pyemotes nr. *scolyti*
- Pityokteines* sp.
 Uropodidae—undetermined sp.
- Pityophthorus carmeli* Swaine
Proctolaelaps sp.
Calvolia sp.
Histiostoma sp.
- Pityophthorus setosus* Blackman
Calvolia sp.
- Pityophthorus* sp.
 Uropodidae—undetermined sp.
Pyemotes nr. *scolyti*
Tyroglyphus sp.
Calvolia sp.
- Pseudohylesinus dispar* Blackman
 Uropodidae—undetermined sp.
- Pseudohylesinus grandis* Swaine
Proctolaelaps sp.
Choriarchus reginus Kinn
Tarsonemus sp.
Pyemotes nr. *scolyti*
- Pseudohylesinus nebulosus* (LeConte)
Pyemotes nr. *scolyti*
Calvolia sp.
Histiostoma sp.
- Scolytus dentatus* Bright
 Uropodidae—undetermined sp.
Tarsonemus sp.
Pyemotes nr. *scolyti*
Cheletophyes sp.
Ereynetoides nr. *scutulis*
Calvolia sp.
Histiostoma sp.
- Scolytus praeceps* LeConte
Tarsonemus sp.
Pyemotes nr. *scolyti*
- Scolytus robustus* Blackman
 Uropodidae—undetermined sp.
Tarsonemus sp.
Pyemotes nr. *scolyti*
Ereynetoides nr. *scutulis*
Calvolia sp.
Histiostoma sp.

Scolytus unispinosus LeConte*Tarsonemus* sp.*Calvolia* sp.*Scolytus ventralis* LeConte*Proctolaelaps* sp.

Uropodidae—undetermined sp.

Tarsonemus sp.*Pyemotes* nr. *scolyti**Ereynetoides* nr. *scutulis**Histiostoma* sp.*Taenoglyptes pubescens* (Hopkins)*Pyemotes* nr. *scolyti*

DISCUSSION

Species of the family Uropodidae are the most widely distributed mesostigmatid mites. Although they are not predaceous on any stage of the bark beetle, they are frequently found in great numbers on the elytral declivity. Trigynaspid mites are most commonly encountered with bark beetles attacking trees in the coastal fog belt. Representatives of the Tarsonemini, many of which parasitize bark beetles, are also frequently encountered. *Pyemotes* nr. *scolyti* has a wide host range and perhaps, because of its large numbers, is an important natural enemy of bark beetles. *Ereynetoides* nr. *scutulis* is the most frequently collected member of the Eleutherengona and may also be an important controlling agent.

PHORESY OF CERCOLEIPUS COELONOTUS AND ITS EFFECT ON BEETLE FLIGHT

The factors affecting phoresy of mites have been studied in only a few species of Mesostigmata (Farish and Axtell, 1966; Rapp, 1959). Our knowledge of the phoretic behavior of trigynaspid mites is confined almost entirely to collection records. These records reveal that dispersal is generally accomplished by adult males and females. Hunter and Davis (1965) studied the life cycle of *Euzercon latus* (Banks) in some detail and found only the adults to be phoretic on passalid beetles. Collection records of *Pleuronectocelaeno drymoecetes* (Kinn, 1968) and *Choriarchus reginus* (Kinn, 1966) also show that the adults are phoretic. With the exception of the work by Atkins (1961), nothing is known of the effect of phoresy on bark beetle flight.

MATERIALS AND METHODS

Frequency of phoretic mites.—*Ips confusus* adults emerging from caged bolts of *Pinus monophylla* were collected individually in gelatin capsules and examined for *Cercoleipus coelonotus* adults. The bolts from which these beetles emerged were collected at monthly intervals at Lake of the Woods, Kern County, California. The sex of some of the beetles carrying *C. coelonotus* was determined by the presence of the pars stridens on the head of the female (Wood, 1961). When more than one *C. coelonotus* was present per beetle, their sex was also determined.

Host specificity.—A survey of the bark beetles in California revealed *Cercoleipus coelonotus* adults to be phoretic on *Ips confusus* and *I. montanus* (Eichh.), both of which belong to Hopping's Taxonomic Group IX (Hopping, 1963). In addition, there were questionable records from *Dendroctonus brevicornis* and *I. emarginatus*. To determine the host specificity of *C. coelonotus*, five males and five females each of ten species of bark beetles were confined in petri dishes on filter paper

with ten *C. coelonotus* adults for two hours. The beetle species tested were: *Ips latidens* (Group O, Lanier, 1967) from *Pinus ponderosa*, *I. mexicanus* (Group I, Hopping, 1963) from *P. muricata*, *I. emarginatus* (Group II, Hopping, 1963) from *P. jeffreyi*, *I. plastographus* (Group III, Hopping, 1963) from *P. muricata*, *I. pini* (Group IV, Hopping, 1963) from *P. contorta*, *I. confusus* (Group IX, Hopping, 1963) from both *P. ponderosa* and *P. monophylla*, *I. montanus* (Group IX, Hopping, 1963) from *P. monticola*, *Dendroctonus brevicomis* from *P. ponderosa*, *D. jeffreyi* Hopk. from *P. jeffreyi*, and *Scolytus ventralis* from *Abies concolor*. Counts of the number of phoretic mites were made every 30 minutes, and each test was replicated five times.

All tests were conducted in a dry atmosphere, under illumination of 500 luxes (measured with a Weston Illumination Meter—Model 756) and at a temperature of $31 \pm 0.5^\circ \text{C}$. The mites used in these and all subsequent tests, unless stated otherwise, were collected from *Ips confusus* in *Pinus monophylla* at Lake of the Woods, Kern County, California, and were held for 24 or more hours on a moist substrate at $3\text{--}5^\circ \text{C}$ prior to testing. Eight additional host specificity tests were conducted: (1) Ten *Cercoleipus coelonotus* adults were confined with ten *I. confusus* and ten *Dendroctonus brevicomis* adults for 30 minutes; (2) Ten *I. confusus* each marked with a dot of paint on the pronotum and ten *I. mexicanus* were confined with ten *C. coelonotus*; (3) Ten *I. confusus* reared from *P. ponderosa* and ten *I. confusus* reared from piñon pine (marked with paint) were exposed to ten *C. coelonotus* collected from *I. confusus* galleries in piñon pine; (4) Test 3 was replicated five times using ten *C. coelonotus* collected from *I. confusus* galleries in ponderosa pine; (5) Ten *I. montanus* (marked with paint) and ten *I. confusus* reared from piñon pine were confined with ten *C. coelonotus* removed from *I. confusus* galleries in ponderosa pine; (6) Test 5 was replicated using ten *C. coelonotus* removed from *I. montanus* galleries; (7) Ten *I. confusus* reared from ponderosa pine and ten *I. confusus* reared from piñon pine (marked with paint) were exposed to ten *C. coelonotus* collected from *I. montanus* galleries in western white pine; and (8) Ten *C. coelonotus* adults were given a choice among twenty *I. confusus*, ten of which were marked with paint.

Initiation of phoresy.—Effect of humidity: Maturation of bark beetle broods is accompanied by marked physical changes in the environment. Most notable of these is a rise in temperature and a lowering of the moisture content of the phloem. Since *Cercoleipus coelonotus* adults attach to *Ips confusus* under a wide range of temperatures ($3\text{--}32^\circ \text{C}$), phoresy may be initiated primarily in response to changes in the relative humidity. This was tested by confining ten mites and ten *I. confusus* adults in the bottom section of plastic petri dishes (100 mm in diam. \times 15 mm) the tops of which were covered with nylon cloth. These units were inverted and taped to bottom sections of petri dishes of the same size, which contained filter paper saturated with various concentrations of KOH (Peterson, 1953). The relative humidities used ranged from 11 to 100 percent. All tests were conducted at 24°C under an illumination of 500 luxes and replicated four times. Mites used for the first three replications were held at 3°C on a saturated substrate for 24 hours prior to testing. Those used in the fourth replicate were held

at 22° C and 50 percent R. H. for one hour prior to testing. Counts were made at 30-, 60-, and 120-minute intervals.

In a similar manner the effect of the moisture level of the substrate on the initiation of phoresy was tested. Fifty *Cercoleipus coelonotus* adults and twenty-five *Ips confusus* were placed together in each of two petri dishes, one of which contained a dry and the other a moist piece of filter paper. Every 30 minutes the mites were counted, removed from the beetles and placed in the other petri dish. Each group of fifty mites was tested four times, twice on a moist substrate and twice on a dry substrate.

Sensory receptor sites: The role of sensory receptors in phoresy was studied using methods similar to those of Farish and Axtell (1966). Adult *Cercoleipus coelonotus* and *Ips confusus* were placed together in a dry environment, and those mites which mounted the beetles were removed and anesthetized with ether. Some of the mites were left intact and the palps or tarsus from one or more legs were removed from others under a magnification of 60× using a 6 mm Zeigler, Needle-type eye knife. Tarsi I, a single tarsus I, tarsi III, or the palps were amputated. The five groups of mites were held at 3–4° C on moist tissue paper for 24 hours prior to testing. Ten mites from each group were placed with adult beetles in a dry atmosphere (40–50 percent R. H.) at 22° C, and the number of phoretic mites in each group observed after 30 minutes. After testing, the mites were returned to a moist substrate and held at 3–4° C for 24 hours before being tested again. In this manner mites were tested on each of three successive days.

Reactions of amputee and intact mites to an insect repellent were studied using an olfactometer which consisted of a glass tube (1 cm in diam. and 25 cm long) inserted into the side of a one-half pint cardboard carton. The ends of the tube were covered with cloth screening after the mites were introduced. The carton enclosed a small petri dish containing filter paper saturated with 20 drops of water or a solution of 80 percent ethylhexanediol (612 insect repellent). Twenty-five mites were introduced into the tube and knocked to the proximal end where they were first exposed to water and then to the repellent. Before being exposed to the repellent, the mites were again knocked to the proximal end of the tube. After 30 minutes exposure to each substance, the number of mites located in the distal 1 centimeter of the tube were counted. This test was replicated three times using mites which had been held for 24 hours on a moist substrate at 3–4° C. Each group of twenty-five mites was tested only once.

Termination of phoresy.—To test whether volatile components of fresh phloem stimulate termination of phoresy, beetles and mites were placed together in a bowl containing dry paper toweling. After one hour beetles carrying mites were removed and divided into two groups and placed in chambers like those used in the humidity tests. The lower section of one unit contained moist filter paper and the other ground phloem from sugar pine. The number of mites still attached was determined after one hour.

A similar test was conducted to determine the effect of odors emanating from fresh frass on the termination of phoresy. In this test the bottom section of the control units contained dry filter paper.

The same units were also used to study the effect of relative humidity on the termination of phoresy. Mites and beetles were placed together for two hours after which ten beetles each carrying one phoretic adult *Cercoleipus coelonotus* were transferred to each of three test chambers with relative humidities of 100, 80, and 61 percent. Relative humidity was controlled by means of filter paper saturated with KOH of different concentrations (Peterson, 1953). These tests were conducted at 24° C under an illumination of 500 luxes. Counts were taken at 15-, 30-, and 60-minute intervals.

Other groups of mites were placed with beetles for 1 to 2 or 3 to 4 hour intervals on dry filter paper before the beetles carrying them were transferred to either dry or saturated filter paper. Two hundred mites were used for each substrate and period of confinement. Counts of the number of mites remaining on the beetles were made after one hour.

Phloem sandwiches constructed from petri dishes (Beanlands, 1966) were used to observe when the mites dismounted. Female *Ips confusus* carrying mites were introduced into petri dishes containing the phloem and bark discs in which nuptial chambers had been excavated by males.

Phoresy and flight initiation.—To determine whether the presence of mites on adult beetles inhibits flexing of the elytra and flight initiation, 150 male *Ips confusus* carrying no mites on their elytra, 150 carrying 1 or 2, and 140 carrying 3 to 5, were divided into groups of ten and placed on dry paper toweling in a petri dish (15 × 2.5 cm) at 500 luxes and $32 \pm 1^\circ$ C. Counts were made of the number of wing flexes occurring within a two-minute period. The beetles used in these tests were collected from ponderosa pine cut at Challenge, Yuba County, California, in January, 1967. Newly emerged beetles were held on wet toweling at 3–4° C for 24 hours prior to testing.

Phoresy and sustained flight.—The effect of the added mass of phoretic mites on beetle flight was studied using a flight mill similar to that used by Chapman (1954) and Atkins (1961). The mill arm was constructed of 1.6 mm aluminum tubing and counterbalanced with solder. Tubing of the same diameter pivoting on wire approximately 0.8 mm in diameter served as a bearing. The radius of the mill arm was 15.9 cm and the circumference of the flight path equaled 1 meter. Beetles were fastened to the end of the arm with a mixture of bees wax and rosin applied to the pronotum (Krough and Weis-Fogh, 1951). Flight mill studies were conducted in a constant temperature cabinet at 30–32° C, 40 percent R. H. and a light intensity of 500 luxes from a 15 watt fluorescent tube and a 40 watt incandescent bulb. The temperature range selected has been found to be the optimum for flight initiation (Borden, 1967).

The beetles used in these tests were collected from ponderosa pine cut at Challenge, Yuba County, California, in January, 1967. Newly emerged beetles were held at 3–4° C on wet filter paper for 24 hours and then allowed to warm to room temperature for 2 to 3 hours in a dry atmosphere prior to testing. Only those beetles which exhibited a strong positive response were selected. Beetles were classified as poor fliers (0–5 minute flights), weak fliers (6–15 minute flights), or strong fliers (flights of over 15 minutes). All mites found clinging to the elytra declivity, coxal joints, or elsewhere on the beetle were removed with a fine forceps.

TABLE 1

SEASONAL OCCURRENCE OF *CERCOLEIPUS COELONOTUS* PHORETIC ON *IPS CONFUSUS*
COLLECTED AT LAKE OF THE WOODS, KERN COUNTY, CALIFORNIA, 1967

Date	Number beetles	Number mites	\bar{X} number mites per beetle	\bar{X} number mites per beetle with mites	Percentage of beetles with mites
I-22	1,139	373	0.33	1.20	27.1
	303	90	0.29	1.21	
	475	187	0.49	1.26	
	1,427	899	0.63	1.54	
	4,207	1,319	0.31	1.37	
	621	141	0.23	1.29	
	6,937	1,395	0.20	1.36	
	24,337	4,012	0.16	1.15	
	2,907	1,164	0.40	1.45	
	2,563	289	0.11	1.14	
Yearly totals and means	4,908	1,025	0.21	1.20	17.2
	50,062	10,934	0.22	1.27	

Mites which may have been beneath the elytra could not be removed without injuring the beetle. However, earlier observations revealed that these were few in number and small in size. Beetles were placed in stender dishes with *Cercoleipus coelonotus* adults and only those with the desired number of phoretic mites were fastened to the mill arm. Twenty male beetles free of mites, twenty male beetles carrying 1 or 2 and twenty carrying 3 to 5 mites were tested. The starting and stopping times were noted for each beetle.

RESULTS

Frequency of phoretic mites.—Adult *Cercoleipus coelonotus* are phoretic on beetles of both sexes. Most beetles carry only one mite but up to eight have been observed. The mites may be all of one sex or mixed. They cling to the beetle by means of the ambulaera of legs II–IV and by the chelicerae, which they clamp onto a seta. They usually attach dorsolaterally on the pronotum and elytra with the elytra being the usual location.

More beetles were found to carry *Cercoleipus coelonotus* between January and June than between July and December (table 1). A highly significant ($P < 0.01$) positive correlation was found between the mean number of mites per beetle and percentage of beetles with mites. Therefore, an increase in the number of beetles carrying mites is accompanied by an increase in the number of mites per beetle. Hypothetical frequencies calculated for a Poisson distribution show that selection of beetles was not entirely random (fig. 1). Of the 50,062 beetles examined,

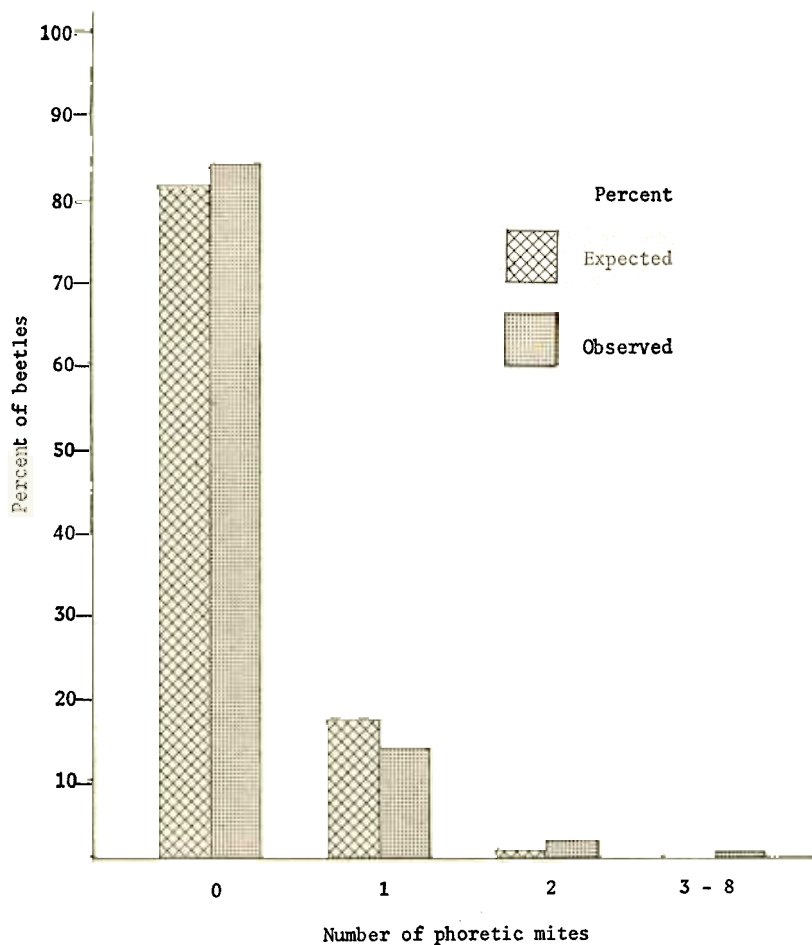


Fig. 1. Expected and observed frequencies of *Cercoleipus coelonotus* phoretic on *Ips confusus* expressed as percent of the entire collection.

8,619 carried *C. coelonotus* distributed as follows: 80 percent only one, 14 percent two, 4 percent three, and 1 percent four.

Host specificity.—The number of phoretic mites was lowest on *Ips latidens* and highest on *I. confusus* and *I. montanus* (table 2). When nonphoretic mites in the *I. mexicanus* test were placed with *I. confusus* from piñon pine, all became phoretic. Phoresy of *Cercoleipus coelonotus* on *Dendroctonus ponderosae* and *Scolytus ventralis* was extremely low. The number of phoretic mites remained relatively constant on all host species during the two hour tests.

When permitted to choose between equal numbers of *Ips confusus* and *Dendroctonus brevicornis*, and *I. confusus* and *I. mexicanus*, *Cercoleipus coelonotus* consistently selected *I. confusus* (fig. 2). *C. coelonotus* removed from *I. confusus* galleries in *Pinus monophylla* selected beetles which had emerged from *P. monophylla* in preference to the same species emerging from *P. ponderosa*. However, *C. coelonotus* removed from *I. confusus* galleries in *P. ponderosa* showed no pref-

TABLE 2

NUMBER OF ADULT CERCOLEIPUS COELONOTUS ATTACHING TO VARIOUS BARK BEETLE SPECIES*

Times (in min.)	<i>Ips latidens</i>		<i>Ips emarginatus</i>		<i>Ips mexicanus</i>		<i>Ips pini</i>		<i>Ips plagiographus</i>		<i>Ips confusus</i> (ex. <i>Pinus ponderosa</i>)		<i>Ips confusus</i> (ex. <i>Pinus monophylla</i>)		<i>Ips montanus</i>		<i>Dendroctonus brevicornis</i>		<i>Dendroctonus ponderosae</i>		<i>Scolytus ventralis</i>	
	No. phoretic	No. tested	No. phoretic	No. tested	No. phoretic	No. tested	No. phoretic	No. tested	No. phoretic	No. tested	No. phoretic	No. tested	No. phoretic	No. tested	No. phoretic	No. tested	No. phoretic	No. tested	No. phoretic	No. tested	No. phoretic	No. tested
30	4	50	12	47	10	49	29	50	35	50	42	50	41	51	44	50	14	48	0	50	1	50
60	6	50	9	48	14	48	28	50	32	50	43	49	41	50	41	50	14	48	0	48	1	50
90	7	50	10	48	15	47	28	50	32	50	40	47	37	45	41	49	19	42	1	44	1	48
120	5	49	6	48	15	47	25	50	31	50	38	47	40	44	39	48	16	41	0	36	2	50
Percentage phoretic	11.0		19.4		28.0		55.0		65.0		84.4		83.6		83.7		35.3		0.5		2.5	

* Total of five replicates.

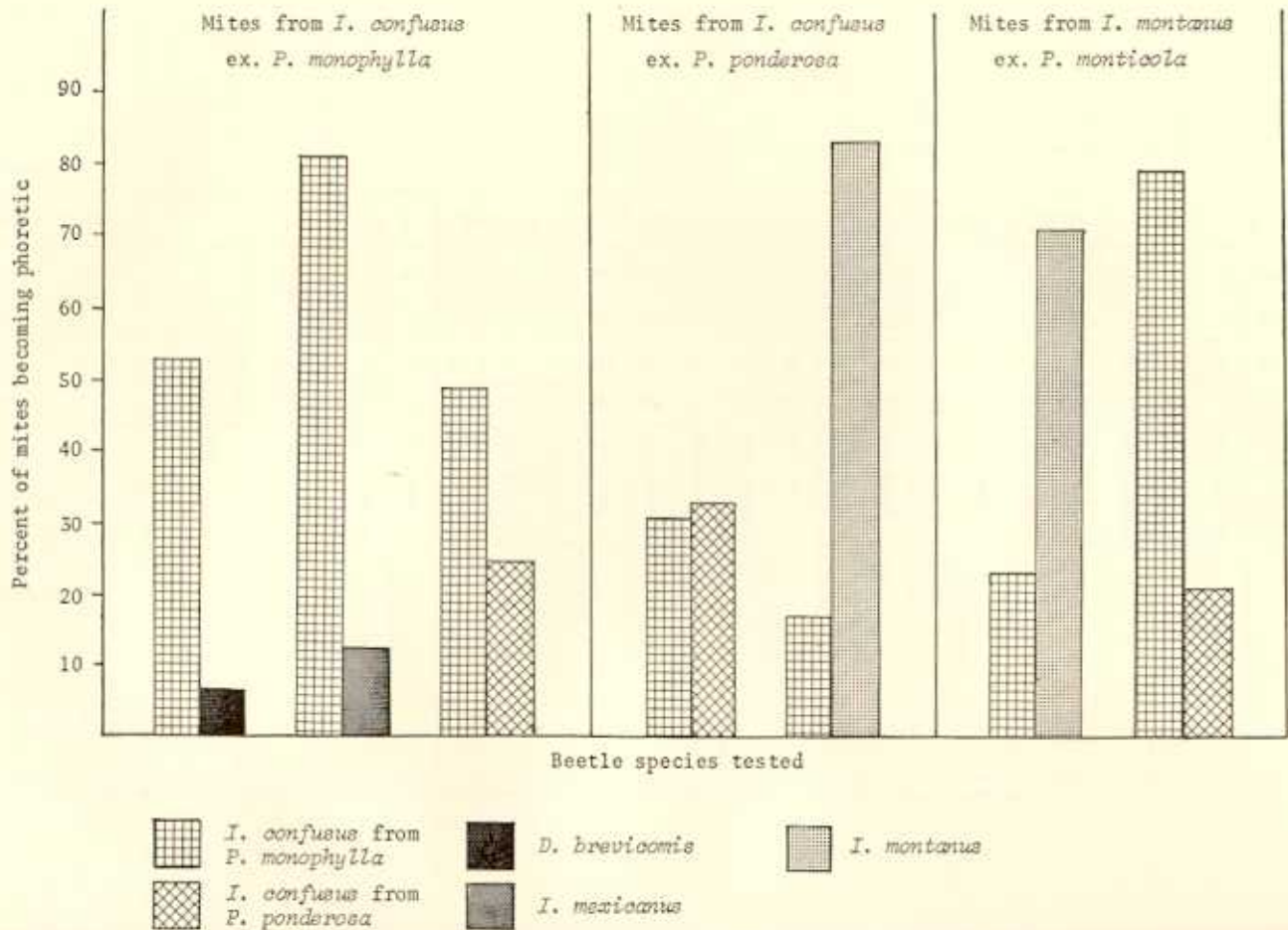


Fig. 2. Host selection by *Cercoleipus coclonotus* reared with *Ips confusus* from *Pinus monophylla*

erence for beetles reared from that host. *C. coelonotus* removed from *I. montanus* galleries in western white pine and from *I. confusus* galleries in ponderosa pine showed a definite preference for *I. montanus* over *I. confusus*. *C. coelonotus* removed from *I. montanus* galleries and present with equal numbers of *I. confusus* removed from ponderosa and piñon pine preferred *I. confusus* reared from piñon pine. Marked beetles were less preferred by *C. coelonotus* than unmarked beetles of the same species (table 3). In the preference studies marked beetles were preferred over unmarked beetles by *C. coelonotus*; therefore these data are conservative estimates of preference except when there were no differences.

TABLE 3

NUMBER OF ADULT CERCOLEIPUS COELONOTUS ATTACHING TO UNMARKED AND MARKED IPS CONFUSUS* FROM PINUS MONOPHYLLA

Replicate	Number mites tested	Number attached to unmarked beetles	Number attached to marked beetles
1	10	8	2
Percentage phoretic			

* Ten marked and ten unmarked beetles used per test.

Initiation of phoresy.—Effect of humidity: Relative humidity did not influence the rate of phoresy (table 4). However, the rate of phoresy on a dry substrate was higher (90.5 percent) than on a wet substrate (67.5 percent) ($\chi^2 = 31.6^{**}$).

Sensory receptor sites: With the exception of those lacking tarsus I, the percentage of intact and amputee *Cercoleipus coelonotus* attaching to *Ips confusus* on the third day was similar to that obtained on the first day (table 5). Phoresy by intact mites ranged from 60 to 100 percent for the 15 replicates; that of palpless mites between 10 and 50 percent for eight replicates, while mites lacking tarsi I did not exhibit phoretic behavior. Mites lacking tarsus I or tarsi III exhibited reduced phoresy. *C. coelonotus* lacking tarsi III did not move as rapidly as intact mites and those lacking tarsus I, and like palpless mites, died earlier. Since mites lacking these appendages became phoretic, yet received injuries comparable to those lacking tarsi I, the lack of phoretic behavior in the latter group cannot be attributed to shock.

Mites with tarsi I or the palps removed were much less repelled by ethylhexanediol than intact mites (table 6).

Termination of phoresy.—Mites did not abandon the beetles in response to the volatile components of fresh sugar pine phloem or beetle frass (table 7) or to an increase in relative humidity (table 8). When the substrate was moist, 49 percent and 81 percent of the mites terminated phoresy after 2 and 4 hours respectively, while on a dry substrate only 16 percent and 30 percent terminated phoresy after

TABLE 4
PERCENT OF CERCOLEIPUS COELONOTUS PHORETIC ON IPS CONFUSUS FROM PINUS MONOPHYLLA
AT VARIOUS R. H. LEVELS AFTER TWO HOURS

Replicate	Relative humidities									
	11	21	31	39	50	61	69	80	90	100
1	83	90	93	80	90	70	70	57	100	43
2	100	97	100	100	97	97	90	100	97	93
3	80	83	83	100	100	97	87	90	80	90
4	83	90	90	80	83	87	87	100	90	93
Mean number mites per observation	86.6	90.0	91.6	90.0	93.2	94.1	83.3	86.6	91.6	80.0

TABLE 5
PHORESY OF ADULT CERCOLEIPUS COELONOTUS ON IPS CONFUSUS AFTER REMOVAL OF TARSUS I, TARS I, TARS I III, OR THE PALPS

Days after surgery	Control		Tarsus I removed		Tarsi I removed		Tarsi III removed		Palps removed	
	Replicates*	Percentage phoretic	Replicates*	Percentage phoretic	Replicates*	Percentage phoretic	Replicates*	Percentage phoretic	Replicates*	Percentage phoretic
1	5	88	5	62	5	0	5	44	5	22
2	5	78	5	64	5	0	4	60	3	30
3	5	84	5	38	5	0	1	40

* Ten mites per replicate.

TABLE 6

NUMBER OF INTACT AND AMPUTEE *CERCOLEIPUS COELONOTUS* REPELLED BY ETHYLHEXANEDIOL

Replicate*	Intact		Tarsi I removed		Palps removed	
	Water	Repellent	Water	Repellent	Water	Repellent
1	7	18	4	7	6	6
2	6	16	0	3	4	5
3	1	12	0	2	2	4

* Twenty-five mites used per replicate per treatment.

TABLE 7

NUMBER OF *CERCOLEIPUS COELONOTUS* REMAINING PHORETIC ON *IPS CONFUSUS* IN THE PRESENCE OF FRESH PHLOEM AND MALE FRASS

Material tested	Number phoretic at start	Number remaining phoretic	Number remaining phoretic in control*
Phloem	57	48	51
Frass	50	43	45

* Same number of mites phoretic at start as in the treatment.

TABLE 8

NUMBER OF *CERCOLEIPUS COELONOTUS* REMAINING PHORETIC ON *IPS CONFUSUS* AT VARIOUS RELATIVE HUMIDITIES

R. H.	Number phoretic after:			Mean rate of phoresy
	15 min.*	30 min. ^b	60 min. ^c	
100	45	42	41	85%
80	48	46	44	96%
61	43	41	41	85%

* Fifty phoretic mites at start.

^b Forty-eight phoretic mites at start.^c Forty-nine phoretic mites at start.

these time intervals. Most mites in a dry atmosphere move rapidly in a tight circular pattern and readily remount the beetles. A few remain motionless beside the beetles, remounting them only when they move. In contrast, mites leaving the beetle and encountering a moist substrate move more slowly and wander away from the host.

Phoretic *C. coelonotus* in phloem sandwiches dismount as the beetle passes through the entrance hole. Only rarely did a mite remain on the beetle entering the nuptial chamber.

Phoresy and flight initiation.—The presence of 3 to 5 adult *Cercoleipus coelonotus* on the elytra of *Ips confusus* significantly reduced the number of wing flexes (table 9).

Phoresy and sustained flight.—Because the elytra of bark beetles are vibrated during flight, it was suspected that the increased mass due to phoretic mites could produce fatigue, which would reduce flight velocity and distance traveled. The average mass of an *Ips confusus* elytron (\bar{X} of 40 male elytra) is $240\mu\text{g}$ and that of an adult *Cercoleipus coelonotus* about $90\mu\text{g}$ (\bar{X} of 42). No significant differences were found between the flight velocities of beetles carrying 1 to 2 mites and those carrying 3 to 5, but the velocity of both groups was significantly less than those free of mites (table 10).

TABLE 9
NUMBER OF WING FLEXES OF MALE *IPS CONFUSUS* CARRYING VARIOUS
NUMBERS OF *CERCOLEIPUS COELONTUS*

Number of phoretic mites	Number tested	Number wing flexes/2 min.	Mean number wing flexes/beetle/min.	t
0	150	369	1.23	
		360	1.20	0.135
	140	267	0.95	2.44*

DISCUSSION AND CONCLUSIONS

Adult *Cercoleipus coelonotus* exhibit a definite preference for *Ips montanus* and *I. confusus* over other species of *Ips*, or species of *Dendroctonus* and *Scolytus* that were tested. This finding is consistent with the collection data for this species, except for the questionable record of *C. coelonotus* from *D. brevicornis*. Because *I. confusus* and *D. brevicornis* often infest the same tree, *C. coelonotus* may become phoretic on the latter species if *I. confusus* is unavailable. The two sibling species now known as *I. confusus* from ponderosa and piñon pine are equally preferred by *C. coelonotus* when only one is present. The host preference exhibited by this mite in decreasing order was: *I. confusus* and *I. montanus* (Group IX), *I. plastographus* (Group III), *I. pini* (Group IV), *I. mexicanus* (Group I), *I. emarginatus* (Group II), and *I. latidens* (Group O). Within Group IX the order of preference appears to be *I. montanus* > *I. confusus*, ex. *P. monophylla* > *I. confusus*, ex. *P. ponderosa*.

When dislodged from a suitable host, *Cercoleipus coelonotus* moves in a tight circle which usually brings it back close to the beetle. At a distance of several millimeters it moves directly towards and remounts the beetle. Such behavior together with the definite preferences exhibited suggests that olfaction is important in host recognition by *C. coelonotus*.

As *Cercoleipus coelonotus* walks, the forelegs are waved back and forth above the substrate while the tips of the palps tap the substrate. This behavior is similar to that of *Macrocheles muscaedomesticae* (Farish and Axtell, 1966) and *Parasitus coleopratorum* (Rapp, 1959). Like most trigynaspid mites, *C. coelonotus* lacks caruncles and claws on tarsi I, but numerous setae occur distally on this segment and the palps.

The mean phoretic rate of 55 percent for mites lacking tarsus I and the absence

TABLE 10

FLIGHT TIME, METERS FLOWN AND VELOCITY OF MALE *IPS CONFUSUS* CARRYING VARIOUS NUMBERS OF *CERCOLEIPUS COELONOTUS*

Number of phoretic mites	Number tested	Meters flown		Flight time (min.)		Velocity	
		Range	Mean	Range	Mean	Range	Mean
0	20	1071-12547	4263.2	21.39-255.14	86.72	30.8-65.6	50.48*
1-2	20	1076-10383	5129.95	21.12-220.64	115.88	29.6-57.3	44.72
3-5	20	704-10573	3419.55	20.29-216.27	79.88	27.6-51.1	41.30

* Significantly different at 0.01 level (Duncan's multiple range test).

of phoresy for mites lacking tarsi I, as compared to 83 percent for intact mites, suggest that *Cercoleipus coelonotus* probably orients by odor intensity discrimination. Mites lacking palps do not respond to repellents and the rate of phoresy initiation is reduced. Sensory receptors which respond to a repellent reside on both the palps and tarsi I, whereas those stimuli which govern the initiation of phoresy are received primarily by tarsi I. However, the reduced rate of phoresy by mites lacking palps suggests that sense receptors on these appendages are also involved in the host perception. A phoretic rate of 50 percent by mites lacking tarsi III is probably due to interference with normal locomotion.

Initiation of phoresy is not influenced by relative humidity or temperature and is reduced by only 20 percent on a moist substrate. Adult mites remain attached even in the presence of fresh phloem and beetle frass and do not terminate phoresy in response to an increase in relative humidity. They remount the beetles immediately on a dry substrate, but phoresy is inhibited on a moist substrate. The termination of phoresy is, in part, a response to contact with moisture. The intensity of this response increases as the length of phoretic association increases, probably as a result of increasing desiccation. Mites phoretic on beetles introduced into phloem sandwiches almost always dismounted as the beetles entered the nuptial chamber and remained on the bark surface for some time before also entering the nuptial chamber. Trees under attack by bark beetles probably have more surface moisture than trees from which the beetles are emerging.

Wing flexing by beetles carrying 3 to 5 *Cercoleipus coelonotus* is inhibited and flight velocity of beetles with phoretic mites is reduced. These findings indicate that phoretic *C. coelonotus* may decrease the dispersal and host finding capacity of their bark beetle host.

BEHAVIOR OF ADULT CERCOLEIPUS COELONOTUS

The behavior of only a few mesostigmatid mite species has been investigated, i.e., *Opionyssus natricis* (Camin, 1953), *Parasitus coleoptratorum* (Rapp, 1959), *Macrocheles muscaedomesticae* (Farish and Axtell, 1966), and *Uroobovella marginata* and *Uropoda orbicularis* (Faasch and Schaller, 1966). The only behavioral study of a trigynaspid mite was performed with *Euzercon latus* (Hunter and Davis, 1965).

MATERIALS AND METHODS

Response to temperature.—Reactions of *Cercoleipus coelonotus* to a linear temperature gradient were observed using an apparatus similar to that used by Camin (1953). A trough, approximately 100 cm long, 5 cm wide, 5 cm deep and constructed of sheet iron was supported at one end by a tripod and the other end was inserted into a canister. The trough was filled with sand, and a glass tube (90 cm long, 1 cm in diam.), sealed at each end, was half buried in the sand. This tube was provided with five vertical tubes 1 cm high and of the same diameter, located in the center and at 10 and 27.5 cm from each end. The sand was saturated with water, and the flame from a bunsen burner was applied to the end of the trough supported by the tripod. The canister supporting the other end was filled with ice and water and the system allowed to stabilize for about 20 minutes be-

fore introducing the mites. A temperature gradient ranging from about 8° C to 52° C was thus established. Temperatures were measured with a thermocouple inserted into the sand next to the outer surface of the glass tube.

Four mites were introduced into each vertical tube and allowed to walk along the horizontal tube for 15 minutes before making an observation. Each test was replicated five times. All mites used in this and subsequent tests were kept on moist filter paper and held at 3–5° C prior to testing.

In addition adult *Cercoleipus coelonotus* were exposed simultaneously to two temperatures in a choice chamber. Water of two different temperatures was placed in each side of a plastic sandwich box (11.4 × 10.3 × 3.3 cm deep), which was divided by a plastic partition cemented to the bottom section. Fifty mites of both sexes were placed on the lid of the box, and the bottom section of a 10 cm petri dish was inverted over the arena. The temperature on each side of the partition was measured with a thermocouple. Observations were made 10 minutes after introducing the mites.

The walking rate and number of turns made by each mite was measured using similar equipment, except the bottom section lacked a partition and graph paper was cemented to the underside of the arena. The walking rate and number of turns of ten male and ten female mites exposed individually to 16° C, 23° C, and 31.5–35° C was recorded.

Response to humidity.—*Cercoleipus coelonotus* adults were placed in cells constructed from the bottom sections of 9 cm plastic petri dishes. One section was covered with organdy cloth and two holes were drilled in the plastic surface. This section was inverted and taped to another dish which was divided by a plastic partition. Filter paper saturated with KOH solutions of different concentrations (Peterson, 1953) was placed on each side of the partition, and fifty mites were introduced through the holes. The following humidity gradients were used: 21–39, 39–50, 50–69, 69–80, 80–90, and 90–100 percent. The mites were held on moist tissue paper for 24 hours at 3° C prior to testing and all tests were conducted at 24° C. Each group of mites was exposed for 7 hours and observed at 30-minute intervals.

The locomotion and turning rate of female mites in uniform environments of 90 and 21 percent R. H. were determined. A square of graph paper was placed on the organdy floor of the above described chamber and the partition excluded.

Thirty palpless mites, thirty mites lacking tarsi I, and thirty intact mites were exposed for 60 minutes on three different days to a humidity gradient of 21–90 percent R. H. Amputations were done on mites anesthetized with ether, after which they were held at 3° C on moist filter paper for 24 hours before testing. Intact mites were also anesthetized and held under the same conditions. Each group consisted of both male and female mites. Amputations were performed with a 6 mm Zeigler, Needle-type eye knife.

Response to light.—Fifty adults were placed in a 9 cm plastic petri dish having half the top section painted black. This unit was illuminated from above by direct and diffuse light of various intensities from a microscope illuminator. Diffuse light was produced by placing a piece of opaque plastic between the illuminator

TABLE 11
PERCENTAGE OF *CERCOLEIPUS COELONOTUS* AGGREGATING IN A GLASS-TUBE
THERMOGRADIENT AT 20-26° C*

Test	Percentage	Minimum temperature	
2	55	10°	32°
4		1.5°	
		13.5°	

* Twenty mites exposed per test.

TABLE 12
PERCENTAGE OF *CERCOLEIPUS COELONOTUS* AGGREGATING AT VARIOUS
TEMPERATURES IN TWO CHOICE TESTS*

Temperature combinations tested (C)									
26°	vs.	32°	23°	vs.	29°	20°	vs.	22°	9° vs. 20°
78		22	68		32	42		58	14 86
									24 76

* Fifty mites exposed per test.

and petri dish, and the heat was removed with a water bath. All tests were conducted at 22-23° C and 52 percent R. H. Light intensities were measured with a Weston Illumination Meter (Model 756).

To test the effect of light intensity on rate of locomotion, twenty adults were exposed at 1, 4, and 48 footcandles. These tests were conducted in diffuse light at 22-24° C and 55 percent R. H. The effect of colored light on rate of locomotion was determined by exposing ten mites to red (Wratten A), yellow (Wratten G) and green (Wratten XI) filtered light at 50 footcandles.

The response of adult mites to a horizontal beam of light from a microscope illuminator was also determined. Light intensity varied between 56 and 860 footcandles in the arena. Twenty-five mites were released at the point receiving 480 footcandles, and their paths were traced on graph paper. Heat effects were minimized by beaming the light through a water bath. All tests were conducted in a darkened room at 21-22° C and 55 percent R. H.

Olfactory response.—Fifty adults were placed in choice chambers similar to those used in the humidity tests, but the bottom section was divided into quarters. Fresh *Ips confusus* frass produced by both male and female beetles boring in *Pinus ponderosa*, freshly ground phloem from *P. ponderosa*, wet and dry filter paper and a total of twenty live male and female *I. confusus* were placed in the bottom section in various combinations. The positions of the mites on the organandy floor were noted at half hour intervals for three hours. These tests were conducted at 20° C and again at 30° C. The turning rate of mites exposed at 30° C to each of these odor sources was also measured.

The olfactory response of mites lacking tarsi I or palps and intact individuals were observed. Thirty mites from each group were exposed simultaneously to ground ponderosa pine phloem and moist filter paper. Each material was presented in 3.5 cm petri dishes and placed in the bottom section of the above chamber. These tests were repeated on three different days and counts were made at 30- and 60-minute intervals. All tests were conducted at 30° C and between tests the mites were held on moist filter paper at 3° C.

Response to contact.—Twenty-five adults were introduced into a sandwich box half of which contained pieces of clear plastic about $\frac{1}{8}$ inch square. After 30 minutes a count was made of the number of immobile mites beneath the pieces of plastic. This test was replicated three times each at 22 and 32° C at 55 percent R. H.

TABLE 13
MEAN TURNING RATE OF *CERCOLEIPUS COELONOTUS*
AT DIFFERENT TEMPERATURES*

Temperature	\bar{X} number turns/sec.
31.5–35° C	1.009 ^a
23° C	
16° C	

* Twenty-five mites exposed at each temperature.

^a Significant from other treatments at 0.01 level (Duncan's multiple range test).

Response to gravity.—A total of twenty-five adult mites of both sexes were placed in the center of a 9-sq in. section of graph paper taped to an inclined drawing board. The direction of their movement was recorded twice at an angle of 30° and once at 70°. Each test was replicated five times. Mites used in the 70° test and in one of the 30° tests were held on moist filter paper for 24 hours prior to testing at 3° C. Mites used in the other 30° test were held on a dry substrate for 1.5 hours at the same temperature prior to testing. All tests were conducted at 22° C and 55 percent R. H.

RESULTS

Response to temperature.—Fifty percent or more of the mites placed in the thermal gradient selected a region between 20 and 26° C (table 11). The preference for temperatures in this range was again exhibited in the two-choice tests (table 12). As mites approached areas having a temperature below 20° C they would tend to stop and become akinetic or move back into the favorable zone. Mites are most active at temperatures between 30 and 35° C (fig. 3). In this range the average rate of locomotion of females and males was 4.6 mm and 7.3 mm per second, respectively. Both sexes become akinetic at 11° C, increased in rate of locomotion up to about 36° C, and decreased abruptly between 36 and 42° C. Several seconds exposure to 50° C resulted in death. Males moved at a faster rate than females, possibly as a result of their greater size. The rate of turning also increased with an increase in temperature (table 13).

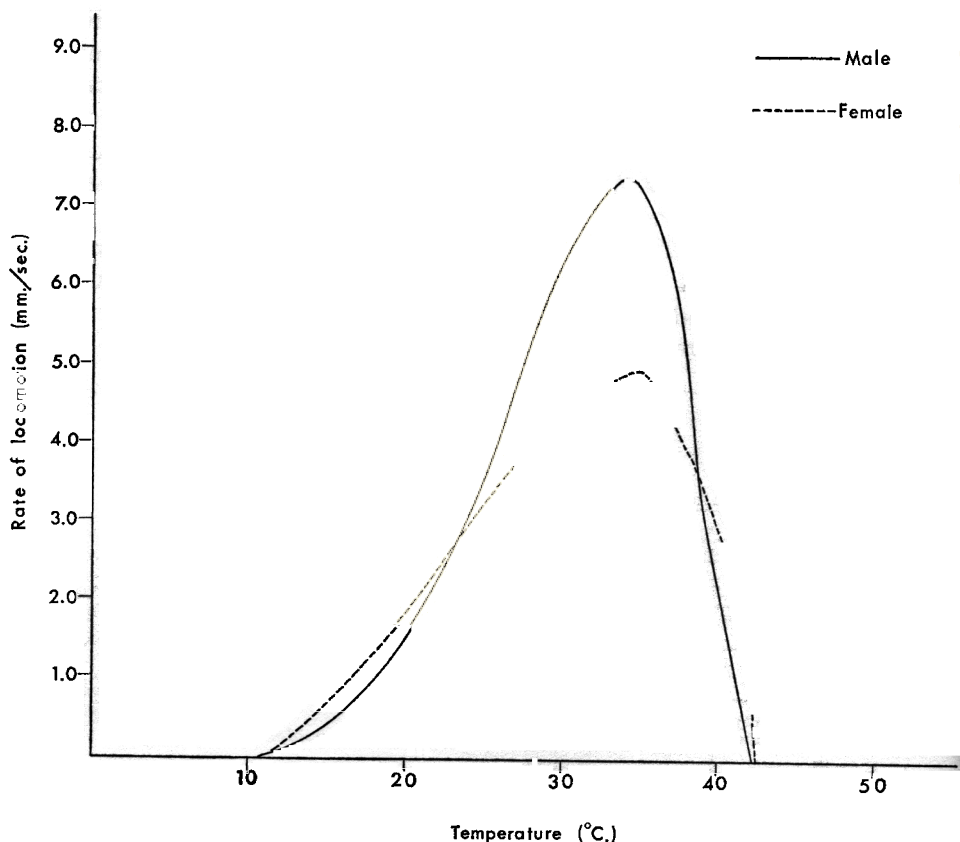


Fig. 3. Rate of locomotion of *Cercoleipus coelonotus* males and females at various temperatures.

Response to humidity.—When permitted to select between two areas at different R. H., *Cercoleipus coelonotus* consistently selected the area of higher humidity and this number tended to increase as humidity increased (table 14). Ninety percent of the mites selected an area at 100 percent R. H. over one at 90 percent R. H., but only 61 percent selected an area of 50 percent R. H. over one at 39 percent R. H. Rate of locomotion was not affected by humidity. In an atmosphere of 90 percent R. H. adults moved at a rate of 3.5 mm/sec and at 21 percent R. H. at a rate of 3.8 mm/sec. The turning rate at the higher and lower R. H. were significantly different (table 15). Intact, tarsiless, and palpless mites responded similarly in humidity gradients ranging from 21 to 90 percent R. H. (table 16).

Response to light.—In direct light of 170–400 footcandles significantly greater numbers of mites aggregated in the dark area (table 17). However, no significant differences were found among the three light intensities tested. Mites moved freely between light and dark areas without exhibiting klinokinetic behavior (Fraenkel and Gunn, 1961).

The mean rate of locomotion at 48 footcandles was significantly greater than that at 1 or 4 footcandles (table 18). Rate of locomotion within a horizontal beam of direct filtered light was random.

TABLE 14
RESPONSE OF *CERCOLEIPUS COELONOTUS* TO HUMIDITY IN VARIOUS GRADIENTS

Times (hours)	Number responding in the following humidity gradients:																	
	21	vs.	39%	39	vs.	50%	50	vs.	69%	69	vs.	80%	80	vs.	90%	90	vs.	100%
1	11		39	14		36	18		32	3		47	1		49	2		48
2	13		37	18		32	22		28	6		44	7		43	5		45
3	18		32	17		33	19		31	7		43	4		46	4		46
4	20		30	19		31	15		35	7		43	4		46	7		43
5	17		33	27		23	19		31	7		43	5		45	8		42
6	12		38	22		28	14		36	14		36	3		47	5		45
7	16		34	21		29	16		34	11		39	4		46	3		47
Percentage	30		70	39		61	35		65	16		84	8		92	10		90

TABLE 15

TURNING RATE OF *CERCOLEIPUS COELONOTUS* IN RESPONSE TO
21 AND 90 PERCENT R. H.

Humidity	Number tested	\bar{X} number turns/sec.
21	20	0.64
90	20	0.49*

*t = 5.29.

TABLE 16

RESPONSE OF INTACT AND AMPUTEE *CERCOLEIPUS COELONOTUS* TO A
GRADIENT OF 21 TO 90 PERCENT R. H.*

Day	Time (in min.)	Intact mites		Palpless mites		Tarsiless mites	
		21%	90%	21%	90%	21%	90%
1	30	7	23	4	26	11	19
	60	6	24	1	29	4	26
2	30	2	28	3	27	6	24
	60	2	28	2	28	6	24
3	30	4	26	10	20	12	18
	60	1	29	2	28	9	21
Mean number mites per observation		3.7	26.3	3.7	26.3	8.0	22.0

* Thirty mites exposed per test.

Olfactory response.—Adults exposed in a choice chamber to adult *Ips confusus*, male and female frass, moist paper, and phloem preferred *I. confusus* adults at 20° C, but at 30° C ground phloem was most preferred (table 19). The turning rate over phloem was significantly reduced from that over the other test substances (table 20). Mites selected wet filter paper over adult *I. confusus* but selected *I. confusus* adults over dry filter paper (table 21).

Intact and palpless mites selected ground phloem over moist filter paper, whereas tarsiless mites displayed no preference (table 22). The response of palpless mites to phloem was consistently less than that of intact mites and was considerably reduced on the fourth day.

Response to contact.—Adult *Cercroleipus coelonotus* tend to become arrested when both their dorsum and venter are in contact with solid objects. Many become immobile with only the anterior edge of the podonotum in contact with a piece of plastic. At 22° C, 42 percent of the mites were arrested while at 32° C, only 8 percent exhibited this behavior (table 23).

Response to gravity.—*Cercroleipus coelonotus* preconditioned on both moist and dry substrates did not exhibit a geotactic response on an inclined surface (table 24).

TABLE 17
RESPONSE OF ADULT CERCOLEIPUS COELONOTUS TO LIGHT AND DARK AREAS*

Light source	Time (in min.)	Number in dark area	Mean number in dark area	χ^2
Diffuse 26 footcandles	30	29	28.0	2.88
	60	31		
	90	26		
	120	26		
Direct 170 footcandles	30	32	32.25	16.82**
	60	34		
	90	34		
	120	29		
Direct 400 footcandles	30	38	31.50	13.52**
	60	22		
	90	34		
	120	32		

* Fifty mites exposed per test.

TABLE 18
RATE OF LOCOMOTION OF CERCOLEIPUS COELONOTUS AT
INCREASING LIGHT INTENSITIES*

Light intensity (footcandles)	Range (mm/sec.)	\bar{X} rate (mm/sec.)
1	1.1-4.4	1.8
	0.8-4.6	

* Twenty mites exposed per test.

* Significant from other treatments at 0.01 level (Duncan's multiple range test).

DISCUSSION AND CONCLUSIONS

Adult *Cercoleipus coelonotus* select a temperature zone of 20 to 26° C by a combination of ortho- and klinokinetic responses. Above 26° C the rate of locomotion and turning increases while below 20° C the turning rate decreases and movement becomes linear. Increased locomotion and turning at high temperatures tend to return the mites to a lower, more favorable temperature. This behavior is similar to that of *Ophionyssus natricis* at high temperatures (Camin, 1953) but unlike *O. natricis*, *C. coelonotus* does not display increased klinokinesis at temperatures below the preferred zone. The slower rate of locomotion and more linear movement at temperatures below 20° C could trap the mites in cooler regions. However, when exposed to two temperatures, one within and one below the favorable zone, *C.*

TABLE 19
RESPONSE OF *CERCOLEIPUS COELONOTUS* TO SEVERAL ODOR SOURCES
IN A CHOICE CHAMBER

Temperature	Time (in min.)	\bar{X} number* responding in two tests to:			
		Wet filter paper	Adult <i>Ips</i> <i>confusus</i>	<i>Ips confusus</i> frass	Ground phloem
20° C	30	11.5	14.5	8.5	15.5
	60	10.5	15.5	12.0	12.0
	90	11.5	13.5	19.0	6.0
	120	9.0	19.0	11.5	10.5
	150	13.0	22.0	9.5	5.5
	180	10.5	22.0	11.0	6.5
\bar{X} number responding	...	11.0	17.75 ^a	11.9	9.35
30° C	30	2.0	4.0	1.5	42.5
	60	1.0	5.5	1.0	42.5
	90	0.5	6.0	1.0	42.5
	120	5.0	9.5	2.0	33.5
	150	3.0	11.0	1.0	35.0
	180	4.0	6.5	4.0	33.5
\bar{X} number responding	...	2.6	7.1 ^a	1.75	38.55 ^b

* Fifty mites exposed per test.

^a Significant from other treatments at 0.01 level (Duncan's multiple range test).

^b Significant from other treatments at 0.01 level (Duncan's multiple range test).

TABLE 20
TURNING RATE OF *CERCOLEIPUS COELONOTUS* IN RESPONSE TO PHLOEM,
WATER, AND *IPS CONFUSUS* FRASS AND ADULTS

Substance	Number tested	\bar{X} number turns/sec.
Phloem	10	0.54*
Others combined	10	0.98

* $t = 3.36$.

coelonotus did not become trapped at the lower temperature. Avoidance of temperatures below 20° C is accomplished by abrupt turning movements observed in the transition zone.

When given a choice between two relative humidity regimes, *Cercoleipus coelonotus* always selects the higher of the two. Since mites lacking palps or tarsi I react similarly to intact mites in a humidity gradient, the hygroreceptors probably are located on other portions of the body. Several species of *Macrocheles*

TABLE 21

RESPONSE OF *CERCOLEIPUS COELONOTUS* TO *IPS CONFUSUS* ADULTS AND WET OR DRY FILTER PAPER IN A FOUR-CHOICE CHAMBER

Number tested	Time (in min.)	Number responding to:				
		Wet paper	Dry paper	Empty section No. 1	Empty section No. 2	<i>Ips confusus</i>
50	30	43	..	5	0	2
	60			6	0	
X number responding	..	43.5 ^a		5.5	0	
50	30	..		1	2	27
	60		16	8	1	
	90		8	8	5	
			9	5	4	
X number responding			13.25 ^a	5.5	3.0	28.25 ^b

^a Significant from other treatments at 0.01 level (Duncan's multiple range test).^b Significant from other treatments at 0.01 level (Duncan's multiple range test).

exhibit similar responses in a humidity gradient (Singh, McEllistrem, and Rodriguez, 1967) but the location of their hygroreceptors is also unknown.

The behavior of adult *Cercoleipus coelonotus* to temperatures above 26° C and below 20° C and at low relative humidities is consistent with the physical environment of this mite. The preferred temperature range and high humidity are probably typical of *Ips* bark beetle gallery systems. Thus, *C. coelonotus* will remain in a favorable environment until the developing beetles open the inner bark to desiccation and higher temperatures.

Examination of *Cercoleipus coelonotus* did not reveal any structures which could be interpreted as light receptors, such as those found in *Ophionyssus natricis* (Camin, 1953). *C. coelonotus* exhibited an orthokinetic response to a direct beam of light. Such behavior could contribute to the aggregation of mites in shaded areas such as beetle galleries or under bark flakes. However, their response to temperature and humidity appears to be more significant in habitat selection.

The olfactory receptors of *Cercoleipus coelonotus* are located primarily on tarsi I as has also been demonstrated in *Ophionyssus natricis* (Camin, 1953), *Parasitus coleopratorum* (Rapp, 1959), *Cosmolaelaps passali* (Mollin and Hunter, 1964) and *Macrocheles muscaedomesticae* (Farish and Axtell, 1966). The lower response of palpsless mites to phloem tissue indicates that these appendages may also bear olfactory receptors as Rapp (1959) concluded for *P. coleopratorum*. Mites lacking a single tarsus I exhibit a reduced phoretic rate, which again indicates that the olfactory receptors are located primarily on tarsi I. Once phoresy has been terminated the response of *C. coelonotus* to phloem volatiles would direct it to an area of high humidity. High humidity tends to inhibit phoresy and maintain mites within the beetle galleries.

TABLE 22
RESPONSE OF INTACT, PALPLESS, AND TARSILESS CERCOLEIPUS COELONOTUS TO PHLOEM
AND MOIST FILTER PAPER IN A TWO-CHOICE CHAMBER

Day	Time (min.)	Number of mites responding								
		Control			Palpless			Tarsiless		
		Phloem	Water	No response	Phloem	Water	No response	Phloem	Water	No response
1	30	24	4	1	20	8	2	7	12	11
	60	24	4	2	20	9	1	8	14	8
2	30	28	2	0	23	5	2	11	8	11
	60	28	2	0	24	5	1	10	9	11
4	30	22	2	6	5	0	25	7	10	13
	60	23	1	6	11	2	17	9	9	12
X number mites/obs.		25**	2.5	2.5	17.2*	4.8	8.0	8.7	10.3	11.0

* Significant from other substance in treatment at 0.05 level (Duncan's multiple range test).

** Significant from other substance in treatment at 0.01 level (Duncan's multiple range test).

TABLE 23

ARRESTMENT OF *CERCOLEIPUS COELONOTUS* IN RESPONSE TO CONTACT WITH SOLID PLASTIC OBJECTS

Temperature	Number tested	Percentage arrested	X ^a
22° C	75	42.6
32° C	75	8.0	22.09**

TABLE 24

RESPONSE OF ADULT *CERCOLEIPUS COELONOTUS* ON AN INCLINED SURFACE*

Replicate	Preconditioned on a dry substrate		Preconditioned on a moist substrate			
	30° angle		30° angle		70° angle	
	Down	Up	Down	Up	Down	Up
1	8	10	12	9	11	13
2	10	11	3	18	9	10
3	13	7	9	14	11	12
4	11	11	8	13	15	6
5	14	9	13	7	13	9
Mean number responding	11.2	9.6	9.0	12.5	11.8	10.0
t ^a	1.21		0.55		1.13	

* Twenty-five mites used per test.

* t_{0.5} = 2.31.LIFE HISTORY OF *CERCOLEIPUS COELONOTUS*

From a survey of the mite fauna associated with *Ips confusus* breeding in *Pinus ponderosa* and *P. monophylla*, both male and female *Cercoleipus coelonotus* were discovered to be phoretic on adult beetles. Immature mites were found only within the beetle galleries. Large size, rapid movements and morphological characteristics of the chelicera suggested that this species was a predator, possibly on some stage of the beetle.

MATERIALS AND METHODS

The behavior and development of mites within bark beetle galleries were observed directly using a modification (Bushong, 1967) of the phloem sandwich technique (Bedard, 1933; Kaston and Riggs, 1937; Reid, 1958, 1962; Hopping, 1961). A uniform piece of phloem tissue from *Pinus ponderosa*, *P. jeffreyi*, *P. lambertiana*, or *P. monophylla* was confined between a plate of glass and a block of wood. The edges of the unit were sealed with paraffin to prevent rapid desiccation. Adult *Ips confusus*, carrying *Cercoleipus coelonotus* adults, were introduced

into the phloem through a hole in the center of the wooden block, which was then covered with one end of a gelatin capsule. All units were kept at 20 to 24° C.

Additional observations were made by placing mites individually in plastic boxes (19 × 23 × 47 mm) on moist blotter paper. Two nylon-covered holes in the covers provided ventilation. The blotter paper was kept moist for 24 hours by placing these units in a plastic box (90 × 167 × 320 mm) and covering them with wet paper toweling. All units were maintained at $23 \pm 1^\circ$ C and examined daily at approximately the same time.

Longevity in a dry atmosphere was determined by placing twenty-five female and twenty-five male *Cercoleipus coelonotus* individually in plastic boxes on dry blotter paper. The boxes were taped and held at 22° C and 58 percent R. H. Observations were made at hourly intervals. Mites used for this test were collected from the elytra of *Ips confusus* and held for at least 24 hours on moist filter paper.

The acceptability of *Ips confusus* eggs and larvae as prey was determined by confining individual mites in plastic rearing boxes with beetle eggs. The number of collapsed chorions or dead larvae, when eclosion occurred, was determined by microscopic examination after 24 hours. The mite was then transferred to a new box containing five fresh eggs. One box containing five eggs but lacking a mite was used as a control. Mites used in replicate I were held on moist blotter paper for at least 24 hours before testing and those used in replicate II were tested immediately after removal from the beetles.

Nematodes of the family Diplogasteridae are associated with *Ips confusus* and were suspected as potential prey for *C. coelonotus*. A colony of these nematodes was maintained on a yeast-phloem substrate. Pieces of phloem with nematodes on the surface were added periodically to plastic rearing boxes containing individual mites.

An attempt was made to establish the incidence of endoparasitic and phoretic nematodes on *Ips confusus* adults. Several hundred beetles from each month's collection were placed in 70 percent alcohol and the undersurface of the elytra examined microscopically for free-living nematode larvae. The abdominal cavity was dissected and examined for the presence of internal parasitic nematodes.

Cytological examinations of squashed testicular and ovarian tissue stained with lactopropionic orcein (Dyar, 1963) were made in attempts to ascertain the sex-determining mechanism of *C. coelonotus*.

RESULTS

Life cycle and longevity.—The life cycle of *Cercoleipus coelonotus* is completed between 18 and 58 days at $23 \pm 1^\circ$ C and 100 percent R. H. (table 25). The average developmental period for both sexes is about 31 days. Since only the adult males and females are phoretic, *C. coelonotus* must complete its development before the beetles emerge. Under similar conditions *Ips confusus* was observed to complete its life cycle within 30 to 40 days. Under natural conditions *I. confusus* requires from 45 to 60 days to complete its life cycle (Struble and Hall, 1955). Of the 102 *C. coelonotus* larvae isolated in the rearing boxes only two survived to the adult stage. One of these remained a protonymph for 21 days and then completed the deutonymphal instar in 6 days. The other individual required 10 days

for each of the two nymphal instars. Although rearing individual mites from egg to adult was unsuccessful, observations of individual mites in phloem sandwiches confirmed the total length of the life cycle recorded in the rearing boxes.

Adult *C. coelonotus* carried by attacking bark beetles will become phoretic again as these parent adults emerge to attack another host tree. Parent adult emergence occurs about 20 to 30 days following the initial attack (Struble, 1955). Adult *C. coelonotus* provided with food will live an average of 16 to 19 days and one female survived as long as 86 days. However, even without food male and female *C.*

TABLE 25
LONGEVITY OF IMMATURE AND ADULT *CERCOLEIPUS COELONOTUS*

Stage	Number*	\bar{X} duration (days)	Range (days)	
			Minimum	Maximum
Egg		7		8
Larva		6		7
Protonymph	9	9		
Deutonymph	13			
Total: egg to adult		31		
Male			3	
Female				

* Number observed completing an individual stage.

coelonotus will live for about 15 days. All stages of *C. coelonotus* may survive the winter but only adults and deutonymphs have been collected from the communal overwintering galleries of adult *I. confusus*.

Behavior within beetle galleries.—Adult *C. coelonotus* wander throughout the parent galleries, tapping the surface with their palps and waving the forelegs. If a mite contacts a female beetle, it will retreat rapidly to the nuptial chamber. The mite may also retreat to the nuptial chamber and enter another gallery or appress its convex ventral surface to the gallery wall and allow the beetle to pass. When not searching the galleries, *C. coelonotus* will preen itself, cleaning the palps with the forelegs and rubbing the chelicerae together.

Adult mites are confined to the parent galleries due to their large size, but larvae and the nymphal instars can sometimes escape the parent galleries as the phloem desiccates and pulls away from the xylem. Molting of the deutonymph to adults may occur in the parent galleries or in the feeding galleries of the teneral adults. When the latter occurs, the mites are in a position to mount the beetles before they bore to the bark surface.

Mating and oviposition behavior.—Young female *C. coelonotus* are often mated prior to becoming phoretic. However, mating also occurs in recently excavated galleries. As many as four attempts have been observed within a 15 minute period. The male apparently senses the presence of a female at a distance of several milli-

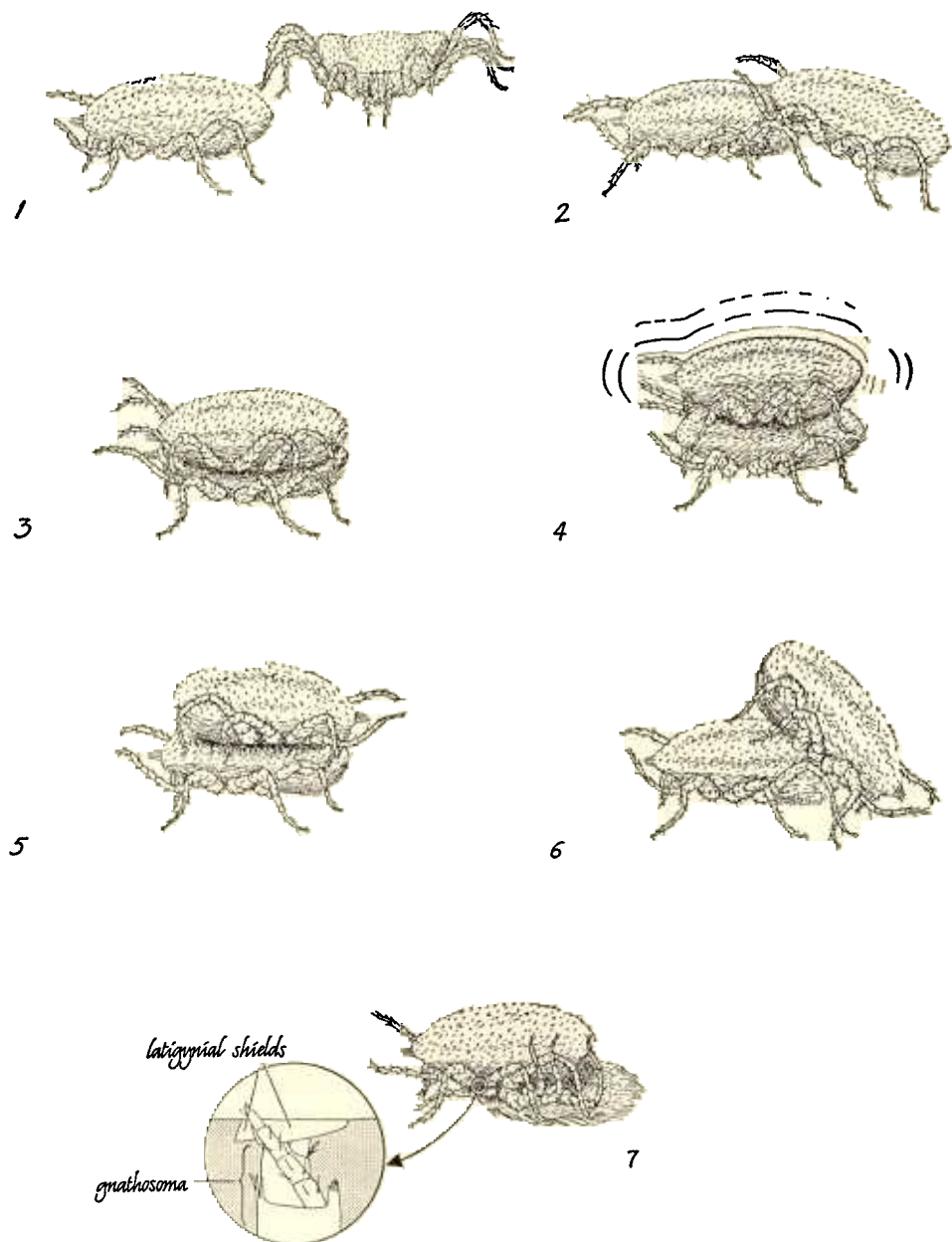


Fig. 4. Mating behavior of *Cercoleipus coelonotus*. 1, Male (anterior view) perceives female. 2-3, Male mounts dorsum of female. 4, Male moves up and down rapidly. 5, Male turns toward posterior of female. 6-7, Male moves over female's opisthosoma onto her venter. 7, Male inserts chelicerae into female's genital orifice.

meters because he moves rapidly towards her and mounts her dorsum (fig. 4:1-3). This is followed by a rapid up-and-down motion by the male (fig. 4:4), after which he turns towards the caudal end of the female (fig. 4:5), and moves rapidly over her opisthosoma onto her venter (fig. 4:6-7). He grasps the edge of her dorsum with legs II to IV and inserts his chelicerae into the female's genital orifice (fig. 4:7). However, no spermatophore was ever observed. Transfer of the spermatophore from the male's genital orifice, which is between legs III and IV, to the chelicerae probably occurs while on the female's dorsum. The male lacks a spermatodactyl; the chelicerai appendages of both sexes appear to be similar. Mating is sometimes interrupted by beetle movement within the galleries.

TABLE 26

SEX RATIO OF LABORATORY REARED AND FIELD COLLECTED *CERCOLEIPUS COELONOTUS* FROM
IPS CONFUSUS GALLERIES IN *PINUS MONOPHYLLA*, LAKE OF THE WOODS,
KERN COUNTY, CALIFORNIA

Sample	Date	Number examined	Percentage females
	Laboratory rearings	206*	49
2	VI-29-1967	1,343	57
3	X-12-1967	700	55
4	XII-7-1967	130	49
Total		2,379	55

* Deutonymphs molting to adults.

Eggs are laid along the wall of the beetle egg galleries, usually in the vicinity of egg niches (pl. 1). The female mite usually covers the eggs with beetle frass and fecal pellets, or when it oviposits on blotter paper, it pulls fibers over the eggs. Eggs were observed in phloem sandwiches 6 to 9 days after introduction of mites. However, some females are capable of ovipositing immediately upon entering the beetle galleries, as young females removed from brood logs and confined in plastic boxes often oviposited during the first day of isolation. Of twenty-nine unfed female mites ovipositing on moist blotter paper, twenty-five deposited 1 egg in 24 hours, three deposited 2 eggs, and one deposited 4 eggs. The number of eggs laid by any unfed mite never exceeded 5, although some survived for 30 days. Fecundity of mites in phloem sandwiches was greater; one female *C. coelonotus* deposited at least 11 eggs during a 16 day period.

The white, finely sculptured eggs are about 288μ long and 226μ wide. From both dorsal and lateral aspects the egg appears elliptical, but in a lateral view the anterior end is more broadly rounded. As incubation progresses, the egg becomes darker and 48 hours prior to eclosion the larva can be seen through the chorion. The setae on the opisthosoma and the legs folded against the ventral surface are visible. The long vertical setae of the opisthonotum are appressed against the body anteriorly. Prior to eclosion the larva cuts the chorion with its

TABLE 27

INCIDENCE OF INFESTATION OF *IPS CONFUSUS* BY FREE LIVING AND PARASITIC NEMATODES

Sample	Date	Location	Number beetles sampled	Number free of nematodes	Number infested with:			Percentage infested
					Free living only	<i>Contortylenchus</i> only	Both	
1	XII-7-1967	Lake of the Woods, Kern Co., Calif.	203	3	132	0	68	98.5
2	II-10-1968	Lake of the Woods, Kern Co., Calif.	267	3	50	1	213	98.8
3	IV-12-1968	Lake of the Woods, Kern Co., Calif.	227	0	100	0	127	100
4	IV-12-1968	12 mi. W Chuchupate Ranger Sta., Ventura Co., Calif.	214	22	39	22	131	89.7
5	VI-26-1968	Mill Potrero Rd., Kern Co., Calif.	200	1	12	1	186	99.5

chelicerae ventrally and posteriorly and escapes by backing out of the chorion. The entire process takes about 25 minutes.

Sex ratio data (table 26) and rearing evidence suggest that the sex-determining mechanism for *C. coelonotus* is not a haplodiploid type. In arrhenotoky the sex ratio would probably fluctuate, exceeding at times a 40-60 ratio. From a total of 2,379 mites examined 55 percent were females. Female mites reared from deutonymphs and isolated from males did not oviposit whereas females dissected from beetle galleries laid eggs. Chromosome counts of tissue from the gonads of male and female mites revealed the 2n number to be 26 in both sexes (pl. 2).

TABLE 28
AVERAGE DAILY CONSUMPTION OF *IPS CONFUSUS* EGGS AND/OR
LARVAE BY *CERCOLEIPUS COELONOTUS* OVER TEN DAYS

Sex		X number of eggs* and/or larvae consumed/day for each of 5 mites			
		I	II	III	V
Female		1.4	0.7	1.1	0.6
	2	0.2	0.9		
Male	1	0.1			

* Each mite was offered five eggs daily.

† Survived less than ten days.

At mitotic metaphase the chromosomes range in size from about 1.5μ to 3.0μ . The similarity of the chromosomes in size and shape at mitotic metaphase did not permit identification of the sex chromosome.

Feeding habits.—Numerous nematode species occur in the galleries of *Ips confusus*, but members of the families Rhabditidae, Allantonematidae, and Diplogasteridae were most commonly encountered. All stages of *C. coelonotus* were observed to feed on free-living diplogasterids and adult mites will also devour the free-living stages of the allantonematid, *Contortylenchus elongatus* (Massey). The incidence of *C. elongatus* and diplogasterids phoretic on *I. confusus* is given in table 27.

Other mites inhabiting *Ips* galleries, such as *Macrocheles boudreauxi* (Krantz, 1965) and *Digamasellus quadrisetus* (Kinn, 1967a) are also known to feed upon nematodes. However, *M. boudreauxi* captures and feeds on other mites and *D. quadrisetus* feeds primarily on immature bark beetles. In contrast, *Cercoleipus coelonotus* appears to prefer nematodes over other prey. In the absence of nematodes, *C. coelonotus* was observed to attack, kill and feed upon *D. quadrisetus*. On several occasions adult females were observed fighting for and feeding upon the body of a dead male *C. coelonotus*. However, it is not known whether this species actually kills individuals of its own species. Immature *C. coelonotus* have been observed to feed upon fungal mycelia.

Individually confined *C. coelonotus* adults occasionally feed upon *Ips* eggs or larvae but seldom take more than one individual per day (table 28). While feed-

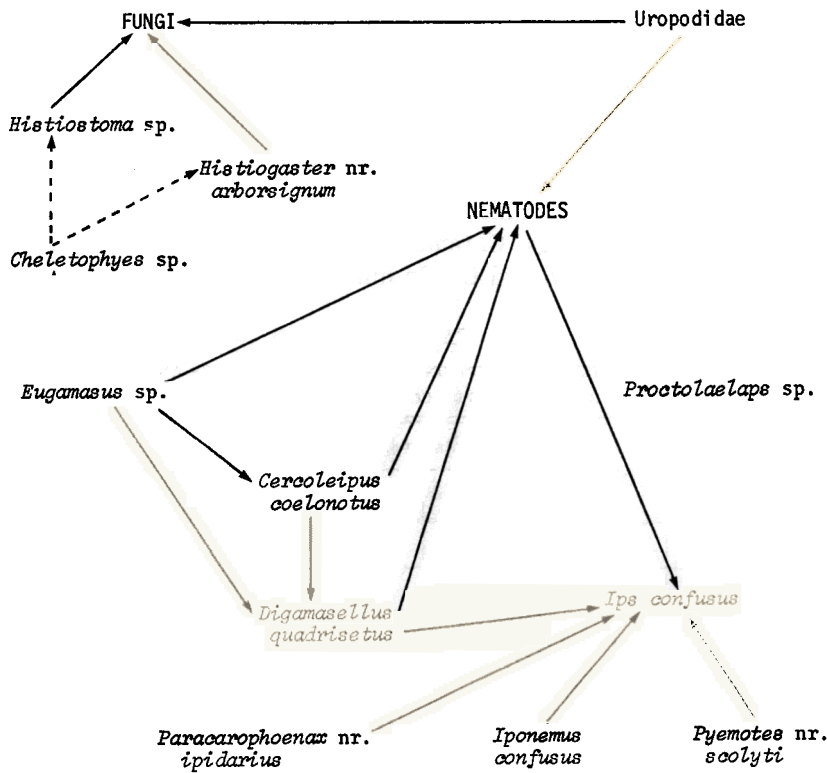


Fig. 5. Food chain relationships among some of the mite species, fungi, and nematodes found in the galleries of *Ips confusus*. Broken lines indicate possible food relationships.

ing the palps are appressed against the egg or larvae and the chelicerae move alternately back and forth. The mite supports itself by legs III and IV and grasps the prey with legs II while the forelegs are raised above the body. Although completely flacid larvae have been found, mites were never observed to suck the entire contents from an egg, although they returned several times to feed. One mite was observed feeding for 15 minutes upon a larva before it was abandoned.

Ceroeleipus coelonotus will walk over nematodes without feeding unless one is contacted with the palps, which are alternately tapped on the substrate. When this occurs the chelicerae are rapidly extended and the nematode is grasped with the chelae and drawn into the oral cavity. This is a rapid process and is easily overlooked by the observer. Dissection confirmed that the nematodes are ingested intact.

Many mites appeared to die of starvation in the rearing boxes although nematodes were plentiful. The searching area may have been too large for the mites to encounter prey. Turnbull (1965) showed that confining prey in a spider's immediate environment did not insure that the prey would be captured. After feeding upon a nematode the mite walks in widening circles tapping the substrate rapidly with the palps. If nematodes are not encountered, it wanders away. Adult *C. coelonotus* often cluster around the caudal region of female *Ips* and

feed upon the numerous immature *Contortylenchus elongatus* that are eliminated by the beetles. The fourth instar larval nematodes are eliminated by the beetle and molt to adults in the beetle galleries (Massey, 1962; Nickle, 1963a).

Other mite associates.—*Cercoleipus coelonotus* phoretic on *Ips* in turn serve as transport hosts for anoetid hypopi. The beetle host is shared with numerous other mite species most of which are not intimately associated with *C. coelonotus*. *Cercoleipus coelonotus* preys upon *D. quadrisetus* while a parasitid of the genus *Eugamasus* appears to be a general predator (Hse, 1964) which was observed to attack, kill, and feed upon adult *C. coelonotus* as well as immature members of their own species. The deutonymphs of this genus are phoretic not only on *Ips* but also on tenebrionids which enter the beetle galleries.

Adult *Proctolaelaps* sp. feed upon beetle eggs, and immature uropodids were seen to feed upon both nematodes and fungal mycelia. *Cercoleipus coelonotus* was not seen preying upon either of these species or the acariform mites present in the galleries. Likewise, predaceous *Cheletophyes*, which often share the same beetle with adult *C. coelonotus*, have not been observed as a predator or prey of *C. coelonotus*.

Some of the known relationships among the various mite inquilines, parasites, and predators found in *Ips* galleries are illustrated in fig. 5. The solid lines represent food chains observed during this investigation and those reported in the literature. The species toward which the arrow points is killed, with the exception of *I. confusus* infested with nematodes. In these fecundity is reduced.

CONCLUSIONS

The ability of adult *Cercoleipus coelonotus* to survive about 15 days without food indicates that some individuals will survive the phoretic period until new galleries are established by the emerging beetles in a new host. Female *C. coelonotus* are probably inseminated prior to becoming phoretic.

Although bark beetle eggs and larvae are destroyed by *C. coelonotus* when confined together in the laboratory, this mite preys primarily on nematodes belonging to the Diplogasteridae and Allantonematidae in the galleries of *Ips confusus*. A single adult *I. confusus* may contain as many as 7,500 larvae and eggs of *Contortylenchus elongatus* (Nickle, 1963a) and within an *Ips* population the infestation level may be 50 percent (Nickle, 1963b) or higher as observed during this study. Massey (1960, 1962) attributed a 58 to 70 percent reduction in the size of *I. confusus* broods to *C. elongatus*. The consumption of endoparasitic nematodes by *C. coelonotus* and its ability to destroy other mites, especially predaceous species such as *Digamasellus quaerisetus*, may reduce mortality of beetle broods.

SUMMARY

Male and female *Cercoleipus coelonotus* are phoretic on *Ips confusus* and *I. montanus* in preference to other bark beetle species, but they do not usually prey upon any stage of the beetle. Phoresy is slightly inhibited when the substrate is moist. As the phloem moisture decreases and temperature increases within the galleries, the mites become more active and readily mount beetles. The increase in temperature which accompanies the drying of the phloem results in greater

locomotor activity of the mite which increases the possibility of contact with beetles. Mites mount the beetles before they emerge, or as the beetles move over the bark surface prior to flight. They grip the beetles with the ambulacra of legs II-IV and fasten the chelicerae on a seta. Usually only one or two mites are found per beetle. Flight initiation of beetles carrying one or two adult *C. coelonotus* is not affected, but flight velocity is decreased.

Once the beetles alight on the host tree the mites dismount and wander over the bark surface before entering the gallery. They walk along the galleries tapping the substrate with the palps and feeding upon nematodes when they are encountered. Mated females oviposit on the gallery walls, often near a beetle egg niche. The eggs are covered with particles of boring dust and broken fecal pellets from the beetle. Adult mites prefer temperatures between 20 and 26° C, aggregate in areas of highest relative humidity, are positively thigmotactic and are attracted to adult *Ips* spp. by olfactory stimuli. Adults are attracted to the odor of fresh phloem and probably enter beetle galleries in response to this odor. Once within the galleries rate of locomotion decreases in response to lower temperatures. A positive taxis to phloem brings the mite into a region of high humidity and the latter inhibits phoresy. They exhibit an orthokinetic response to clear light but do not respond to color or gravity.

The life cycle of *C. coelonotus* is completed in 18 to 58 days at $23 \pm 1^\circ$ C and 100 percent relative humidity. The average time required from oviposition to molting to the adults is 31 days. Average durations of each stage are: egg incubation, 7 days; larva, 6 days; protonymph, 9 days; deutonymph, 9 days. Nutrition appears to be the primary factor influencing the length of each stage. Virgin females in the absence of males will not oviposit and the 2n chromosome number is 26 for both sexes which indicates that the sex-determining mechanism is not a haplo-diploid type.

Adults prefer to feed upon the free-living instars of *Contortylenchus elongatus*, an important endoparasitic nematode of *Ips confusus*, and all stages will feed upon nematodes belonging to the Diplogasteridae. Adult *C. coelonotus* will also feed upon an important mite predator of *I. confusus* eggs and larvae, *Digamasellus quadrisetus*.

ACKNOWLEDGMENTS

The critical review of this paper by Drs. J. H. Oliver, Department of Entomology, University of Georgia, Athens; D. L. Wood, Division of Entomology, University of California, Berkeley; and C. H. Hand, Department of Zoology, University of California, Berkeley, and the helpful suggestions offered by fellow graduate students of the Division of Entomology during the course of this investigation are sincerely appreciated. I also wish to thank Drs. E. W. Baker, Division of Insects, United States National Museum, Washington, D.C.; E. Cross, Department of Biology, Northwestern State College, Natchitoches, Louisiana; P. E. Hunter, Department of Entomology, University of Georgia, Athens; H. W. Hurlbutt, Department of Biology, West Virginia University, Morgantown; and J. P. Woodring, Louisiana State University, Baton Rouge, for identifying mite species. I am grateful to Dr. Donald E. Bright, Entomology Research Institute, Canada Department of Agriculture, Ottawa for identifying many of the bark beetle hosts; Dr. G. O. Poinar, Division of Entomology, University of California, Berkeley, for identifying nematode species; Dr. J. C. Moser, United States Forest Service, Alexandria, Louisiana for specimens and much useful information; Mr. A. A. Blaker, Scientific Photographic Laboratory, University of California, Berkeley, for much of the photographic work; and Mrs. J. L. Morley, Scientific Photographic Laboratory, University of California, Berkeley, for drawing fig. 4.

Special appreciation is expressed to my wife, Yvonne, for her assistance with the typing of this manuscript and to both my wife and son, Neil, for their assistance on collecting trips.

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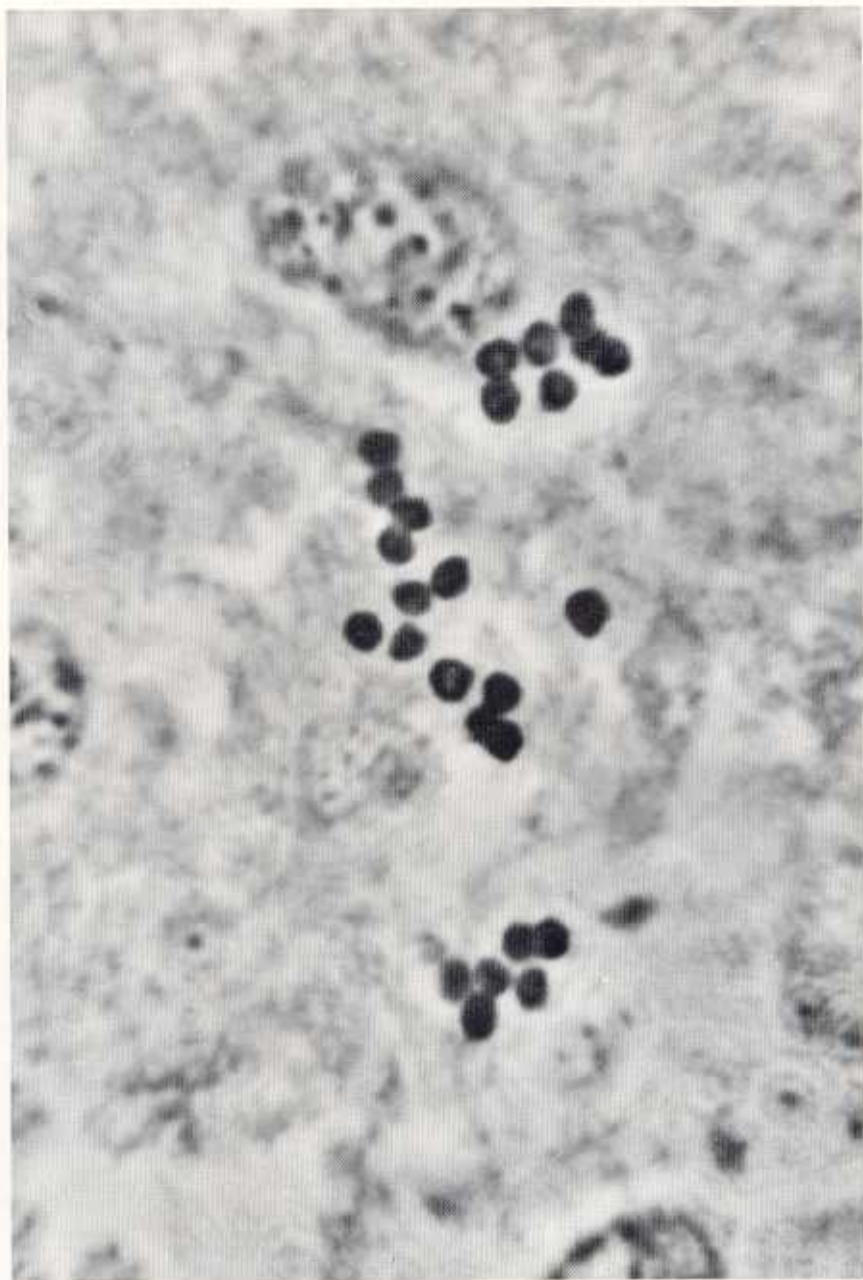
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PLATE 2



Chromosomes from *Cercolcippus coelonotus* ovarian tissue at mitotic metaphase.